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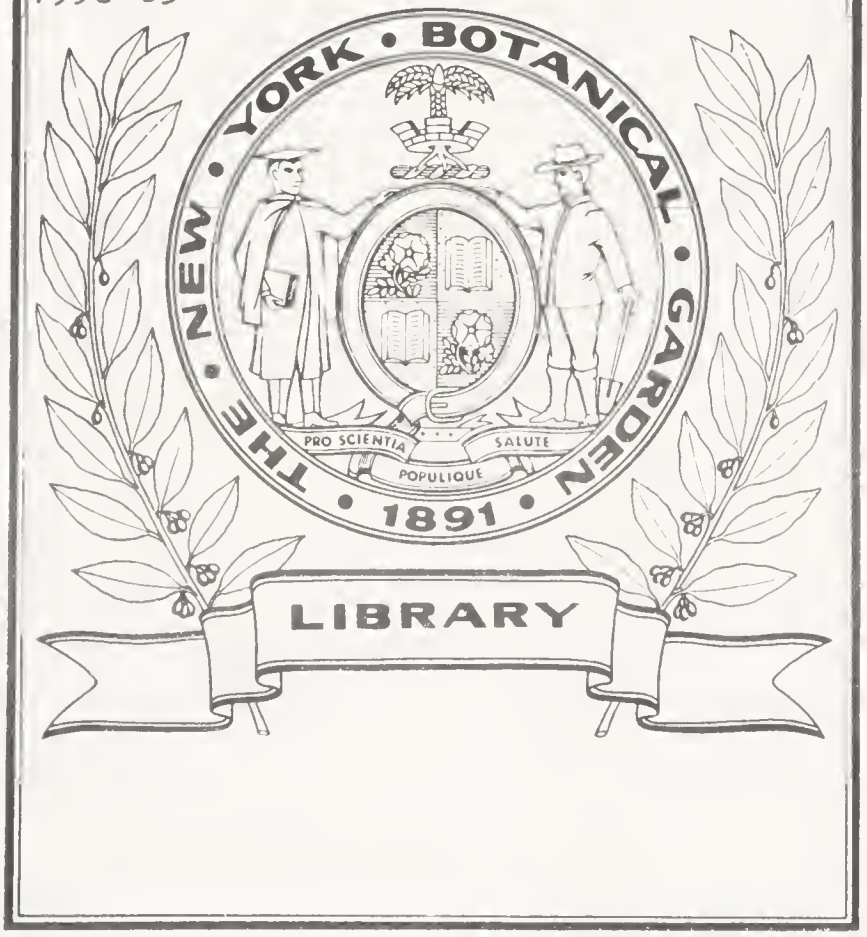

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Memoirs

of

The Torrey Botanical Club

Vol. 21, No. 1 August 29, 1958

Editor
MURRAY F. BUELL

MONOGRAPH OF THE GENUS ARGEMONE FOR NORTH AMERICA AND THE WEST INDIES

By

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Published for the Club by
THE SEEMAN PRINTERY
Durham, N. C.

X11
E588
vol. 21
1958-63

Memoirs of the Torrey Botanical Club

Volume 21

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MONOGRAPH OF THE GENUS ARGEMONE FOR NORTH AMERICA AND THE WEST INDIES[1]

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[1] Publication costs of this paper were met by the Torrey Botanical Club and the Guggenheim Foundation.

Historical Review of the Taxonomic Literature

The first species of *Argemone* known to science was *A. mexicana* which was grown by John Gerard from seeds brought to him from St. Johns Island, West Indies, in 1592. Caspar Bauhin (1596, p. 311) was the first to publish a description of the species, under the name *Papaver spinosum*. His description was followed a year later by that of Gerard (1597, p. 993) who illustrated and discussed the species under the name *Carduus chrysanthemus peruanus*. Tournefort (1694, 1700) established the generic name *Argemone* in its modern sense. In it he placed only one species, Bauhin's *Papaver spinosum* which he referred to as *Argemone mexicana*. Species previously treated under *Argemone* were transferred by Tournefort to the genus *Papaver*.

Linnaeus (1753) included *Argemone* in his Polyandria Monogynia. He listed three species, viz., *A. mexicana*, *A. armeniaca* and *A. pyrenaica*. The genus, as a consequence, was unnatural in the Linnaean sense, since the latter two species according to all subsequent authorities belong to the genus *Papaver*. Lamarck (1783) re-establish *Argemone* in the Tournefortian sense by referring the alien elements to *Papaver* (see Poiret, 1804, p. 118). Lamarck (1783) was also responsible for first recording a white flowered "variety" of *A. mexicana*. This could be none other than the plant subsequently referred to by Lestiboudois (1799) as *Argemone alba*, a nomen nudum. The same white-flowered species was validly published as *A. albiflora* by Hornemann (1815).

The next *Argemone* to be described was *A. alba* James (1823), a later homonym of *A. alba* Rafinesque (1817). *A. alba* James falls into synonomy under *A. polyanthemos* in the present paper.

The next species of *Argemone* known to science were introduced into Europe by means of seeds from Mexico. These species, all described from cultivated plants, were *A. platyceras* Link & Otto (1830), *A. ochroleuca* Sweet (1829), *A. grandiflora* Sweet (1829), and *A. intermedia* Sweet (1830). All of these are clearly defined species except *A. intermedia* which was not illustrated as were the others; nor were specimens preserved in-so-far as I can determine. As a result, the correct application of this name has never been properly established.

The next species of *Argemone* to be described was *A. hispida* Gray (1849), followed by *A. munita* Dur. & Hilg. (1854). After this date no new discoveries were made in the genus until Greene described *A. corymbosa* (1886).

The first comprehensive revision of *Argemone* is that prepared by Dr. David Prain based upon specimens in the herbaria of London, Paris and Geneva, published in 1895. This revision is notable primarily for its

exhaustive coverage of the literature up to that time. All later students of the genus should refer to Prain's monograph in compiling bibliographic data, especially with regard to *A. mexicana*. Prain's discussion of the pre-Linnean and later literature is also of great value. Since he was a student of the family Papaveraceae his ideas of generic inter-relationships merit special attention. With regard to *Argemone* itself, Prain was extremely reluctant to describe new forms. He recognized a total of six species and five varieties, not counting the typical varieties, for a total of eleven named taxa for the world. He did not consider his treatment of the species of *Argemone* to be definitive in the least, stating (l.c., p. 177-178) that "the 'species' of this paper are in reality aggregations of forms that probably most botanists would recognize as specifically distinct." Two of the taxa treated by Prain are not considered in the present treatment, viz., *A. alba* var. *glauca*, really a distinct species endemic to the Hawaiian Islands, and *A. platyceras* var. *chilensis*, also a distinct species with at least two distinguishable subgroups. Still another distinct South American species with possibly two sub-groups was submerged in *A. mexicana* var. *ochroleuca* by Prain. Of the remaining nine taxa recognized by Prain, only one was new. This was *A. intermedia* var. *stenopetala*, certainly distinguishable, but more properly treated as a subspecies of *A. ochroleuca*. *A. fruticosa* and *A. grandiflora* were justifiably upheld by Prain, as was *A. mexicana* which, with the removal of var. *ochroleuca*, is a homogenous species. *A. mexicana* var. *ochroleuca* of Prain, when restricted to Mexico and Central America and when raised to full species status is probably biologically sound. *A. intermedia* var. *typica* Prain was not adequately typified and included a series of forms better treated as distinct species. *A. platyceras* var. *typica* Prain included not only *A. platyceras* L. & O., but several other taxa better treated as distinct species. *A. platyceras* var. *hispida* as circumscribed by Prain includes two components, true *A. hispida* and *A. munita* subspp. Finally, *A. alba* var. *typica* Prain, exclusive of Texas specimens, is *A. alba* Lestib., a name which should be replaced by *A. albiflora* Hornem. From this brief summary, it is evident that, with a few notable exceptions, Prain's understanding of the species of *Argemone* is reasonably valid today. Several of the taxa herein described as new were briefly mentioned by Prain, but in the light of his very limited knowledge of these groups he understandably refrained from formally proposing them as new.

During his lifetime, Dr. Edward L. Greene described several species of *Argemone*. *A. corymbosa* was described in 1886, *A. bipinnatifida*, *A. gracilenta* and *A. leiocarpa* in 1898, *A. sanguinea* and *A. squarrosa* in 1899, and *A. pleiacantha* in 1908. Of these, *A. sanguinea* is a new name for *A. platyceras* var. *rosea* Coulter; *A. leiocarpa* is the glabrous fruited form

of *A. mexicana* and seems to have been prompted by its mention in Prain's monograph, and *A. bipinnatifida* is clearly a synonym of *A. hispida* Gray. The remaining names were applied to good species previously not distinguished by taxonomists. Greene's published writings about *Argemone* are not extensive. His ability to recognize new forms does, however, indicate a wide familiarity with the species in nature.[1]

J. N. Rose (1903) published a brief but excellent account of the Mexican species of the *Argemone* with which he was familiar. He recognized eleven species for the area, one of which was newly described, viz., *A. arida*. The specimens referred to *A. hispida* by Rose are more correctly placed in *A. echinata* as herein described; those referred to *A. munita* actually belong to *A. pleiacantha* which was not distinguished until 1908. *A. stenopetala* (Prain) Rose is best left a subspecies of *A. ochroleuca*. The remaining names taken up by Rose agree in their application with that set forth in the present paper. It is notable that Rose did not apply the name *A. intermedia* to any Mexican species although this species was reputed to be a native of Mexico at the time of its original cultivation in England.

The most recent revision of *Argemone* for the world is that of Friedrich Fedde published in 1909 in Das Pflanzenreich. This revision is based very largely upon Prain's earlier publication, but embodies several advances especially with regard to the incorporation of several of E. L. Green's proposals. *A. corymbosa* is given recognition, but as a variety of *A. intermedia*. Similarly *A. gracilenta* and *A. pleiacantha* are recognized, but only as varieties of *A. platyceras*. *A. squarrosa* is given full species standing. On the other hand, several proposals seem to the present writer to be without merit. For example, Greene's *A. leiocarpa* is given full species standing and is divided into two varieties. Probably *A. leiocarpa* is no more than a form of *A. mexicana*. *A. ochroleuca* Sweet is left as a variety of *A. mexicana* regardless of differences which are of specific weight in *Argemone*. *A. purpurea* Rose is provided with a description for the first time without recognizing that it is synonymous with *A. sanguinea; A. sanguinea* is submerged in *A. platyceras*. *A. platyceras* L. & O. is not properly delimited and includes a mélange of forms more properly treated as distinct species. *A. intermedia* Sweet is allowed to stand without adequate typification and includes several distinguishable taxa. Never-the-

[1] In Greene's herbarium at Notre Dame University there is a handwritten manuscript entitled "Observations on Argemone," by Greene. This in actuality is a commentary on Prain's monograph and evidently was never completed or published. After some critical remarks about the lack of field knowledge of *Argemone* by Europeans and most Americans the manuscript ends with the words: "Meanwhile let me offer, as an original contribution to the knowledge of the genus, some geographic facts." No new information of value is included in the completed section of the manuscript.

less, Fedde's contribution to our understanding of *Argemone* is considerable and has the merit of being generally conservative. Its deficiencies may be attributed primarily to a lack of adequate study material upon which to base a sounder circumscription of species and varieties. Also, Fedde did not have a first hand knowledge of the distributional aspects of the species of *Argemone* and much unnecessary lumping of taxa and incorrect disposition of individual specimens may no doubt be traced to this factor.

History of Cultivation

The first *Argemone* to be introduced into Europe was *A. mexicana* first cultivated by Gerard. On the authority of Aiton (1811), Sweet (1830) and Loudon (1830), all of whom evidently refer back to Clusius, the date of introduction was 1592. The first mention of the species in literature was by Bauhin (1596) and by Gerard (1597), the latter having received seeds of the species from St. Johns Island in the West Indies. It has been in more or less continuous cultivation in Europe since its introduction. The next species to be introduced into cultivation appears to have been *A. albiflora,* first mentioned by Lamarck (1783) as the white-flowered variety of *A. mexicana.* The actual date of introduction was prior to 1783, but I know of no account of exactly when or under what circumstances it was introduced into Europe. It was introduced to the gardens at Copenhagen in 1812 according to Hornemann (1815), and into England in 1820 (Sweet, 1830) or 1821 (Loudon, 1830). It evidently enjoyed its greatest popularity in gardens before the introduction of other species between 1827 and 1830. *A. ochroleuca* was introduced into Europe before 1790 according to Prain (1895, pp. 208, 328) but was not continued in cultivation. Prain's basis for this statement was a specimen cultivated at Paris in the eighteenth century and preserved in the A. L. Jussieu herbarium. The species was again introduced, into England, in 1827 according to Sweet (1830) and has since remained in cultivation. *A. grandiflora,* the best of the white-flowered species for gardens, was also introduced into England in 1827 according to Sweet (1830), Loudon (1830) and Prain (1895, p. 333). It has been in cultivation since that date. Another species, *A. intermedia,* was introduced into England from Mexico in 1828, according to Sweet (1830, 1839). I have been unable to establish the identity of this species, but it almost certainly is not the same as the species of the Great Plains to which the name has been applied for the past sixty years (*A. polyanthemos* of this paper). At any rate, *A. intermedia* Sweet did not continue in cultivation and seems to be listed nowhere else in the literature of the period. The white-flowered species of the Great Plains, *A. polyanthemos,* was introduced into England from Colorado in 1877 by J. D. Hooker and

was figured by Hooker (1878) under the name *A. hispida*. It was not continued in cultivation. *A. platyceras* was introduced into Europe in 1829 according to Link & Otto (1830) and flowered at Berlin in 1829 and 1830 without, however, bearing seeds. Prain (1895, p. 365) states that *A. intermedia* var. *stenopetala* (i.e., *A. ochroleuca* subsp. *stenopetala* of this paper) was cultivated by Cosson from seeds taken from specimens sent to him by Pringle. Specimens of the garden plants are preserved, according to Prain, in the Cosson herbarium at Paris. The date of cultivation was not earlier than 1885 since this is the year Pringle first collected the subspecies.

The period of greatest popularity of *Argemone* in the gardens of Europe was 1827-1840 according to Prain (1895, p. 129). In the United States, none of the species of this genus has ever achieved any great popularity in gardens. *A. mexicana* and *A. grandiflora* have been cultivated more or less continuously but never widely. *A. platyceras*, *A. sanguinea*, *A. munita* subsp. *munita*, *A. polyanthemos* (as *A. intermedia*) and probably other species, have also been cultivated occasionally. Species which merit further attention as subjects for gardens are *A. sanguinea*, *A. polyanthemos* and *A. aenea*.

Medicinal Use

The use of *Argemone* for medical purposes is recorded by numerous authors. In Puerto Rico, Cook and Collins (1903) report that the seeds of *A. mexicana* are employed as a purgative, as a substitute for ipecacuanha, and that the juice is used in the treatment of ophthalmia. This species and others are similarly utilized throughout Latin America and also for a wide variety of other ailments. The active principles in *Argemone* appear to be alkaloidal in nature, but very little scientific work on their identification and medicinal uses has yet been done.

Common Names

A. mexicana was referred to by Gerard (1597) as "The golden Thistle of Peru." The seeds received by him carried the Spanish name of the day "Figue del Inferno." In Britton & Brown (1913) *A. mexicana* is termed the "Mexican Prickly or Thorn Poppy," also "Bird-in-the-bush, Devil's fig, Yellow, Flowering or Jamaica thistle." In Jamaica, according to Fawcett & Rendle (1914), *A. mexicana* is called "Prickly Poppy," "Gamboge Thistle," or "Mexican Thistle." In the Bahama Islands, according to Britton & Millspaugh (1920), *A. mexicana* is termed the "Donkey thistle" or "Mexican Poppy." In Bermuda, Britton (1918) states that the names "Mexican Poppy," "Prickly Poppy," "Stinging Thistle," and

"Queen Thistle" are applied to *A. mexicana*. In Mexico, according to Martínez (1937) the name "Cardo" is applied to *A. mexicana* as well as to other species; "Cardo Santo" is used for *A. mexicana* and *A. fruticosa; A. grandiflora* is called "Chacalote" or "Chicalota Grande"; "Chicalote" is used for *A. mexicana, A. ochroleuca* and also *Bocconia* sp.; and "Chicalotl" is used exclusively for *A. mexicana* and *A. ochroleuca*. Standley & Steyermark (1946), for Guatemala, list the following names for *A. mexicana:* "Chicalote," "Cardosanto," "Cajhuoc," "Ixmucur," "Kixatucan," "Sajouix," and "Cahhouc." In North America north of Mexico the common name "Prickly Poppy" is used for all species of *Argemone;* when reference is made to one of the yellow-flowered species, usually *A. mexicana*, it is usually termed "Mexican Poppy."

Geographical Distribution

Argemone is an exclusively American genus with the exception of one species endemic to the Hawaiian Islands. In North America there are twenty-three species recognized in the present paper. These are found along the coastal areas of southeastern and southern United States to Texas, thence westward to the Pacific and northward across the Great Plains to western South Dakota and southern Montana; in the far west *Argemone* is found throughout the desert regions and northward across the Great Basin to northern California and southeastern Oregon. *Argemone* is present throughout Mexico and Central America except in the higher mountains, and throughout the islands of the West Indies. In South America there are four or five recognizable taxa found in Chile, Argentina, Uruguay, Paraguay, Bolivia and northward along both coasts to the Isthmus of Panama. *Argemone mexicana* is introduced into all tropical and subtropical regions of the world; *A. ochroleuca* is introduced into Australia. In North America the species of this genus occur almost exclusively in regions of low rainfall at elevations of near sea level to 8,000 feet, rarely more; when they occur in areas of moderately heavy rainfall they are found only in soils of low water-holding capacity. Many species spread rapidly into newly disturbed areas; many are incipient weeds in fields and about dwellings within their natural distributional areas and in adjoining regions. For this reason the absolute distributional boundaries of many species before the introduction of modern agricultural practices is difficult if not impossible to establish.

Man has played an important role in the dispersal of the seeds of *Argemone* in the past. This role has probably been passive in most instances; either the seeds have been carried along as contaminants in the seed of crop plants of a similar size or the seeds have been mixed with

other materials transported from place to place; in the case of *A. mexicana* the seeds probably have been carried from port to port in ship's ballast. In the southwest and in Mexico *Argemone* is often closely associated with cultivated fields and dwellings of man. It is avoided by all livestock, and because of the prickliness of its stems and leaves survives successfully where most other plants would be eliminated. Man has undoubtedly played an active role in the dispersal of *A. mexicana* and *A. ochroleuca* because of the supposed medicinal properties of these plants previously mentioned.

The usual natural forces of wind and water also are effective in the dispersal of the seeds of *Argemone*. Certain features of the seed seem to the writer to be especially important in their dispersal by water. First, the seeds are covered by a thin coat of wax which inhibits the absorption of water; then, the shallow pits in the seed coat appear to act as air traps when the seeds are placed in water; finally, in the seeds examined, there was a small air pocket under the seed coat beneath the micropyle. The first of the features prevents the immediate water-logging of the seed when it comes into contact with water; the latter two features add to its buoyancy. Taken together they would appear to enhance the chances of water transport of the seeds under favorable conditions. When the seeds of *Argemone* are placed in water in the laboratory, they float on the surface for one to several days.

Generic and Intrageneric Relationships

Argemone is set apart from other genera of the Papaveraceae by several important features including the basically trimerous arrangement of the sepals and petals, the presence of sepal horns, the united styles and the mode of dehiscence of the capsules. None of these features taken individually is peculiar to *Argemone* but their presence in combination in *Argemone* forms the basis for the taxonomic delimitation of the genus. For example, trimery and horned sepals are found in species of *Papaver;* capsules of *Meconopsis* and *Romneya* dehisce much as they do in *Argemone;* united styles are found in *Meconopsis*. *Argemone* is placed in the tribe Papavereae by Fedde (1909) along with *Meconopsis*, *Papaver*, *Canbya*, *Cathcartia*, *Roemeria* and *Glaucium*. The genus appears to be most closely related to *Papaver* and *Meconopsis*.

Some effort has been made without success to discover groupings of species in *Argemone* which might form the basis for establishing sections within the genus. There is no evidence for the existence of groupings of this magnitude. Some poorly definable alliances among species may, however, be pointed out, but there are many species which cannot be assigned with any assurance to any alliance, nor do the alliances themselves appear

to have any high degree of reality. For example, *A. mexicana* and *A. ochroleuca* and possibly also *A. aenea* and *A. superba* form one alliance; *A. echinata, A. squarrosa, A. aurantiaca, A. pleiacantha, A. hispida* and *A. munita,* in part, and possibly *A. platyceras* form another alliance; *A. albiflora, A. polyanthemos, A. grandiflora* and *A. gracilenta* form still another alliance. Several species such as *A. fruticosa, A. corymbosa* and *A. subintergrifolia* seem to have no very close relatives; the remaining species do not fit well into any of the above alliances, yet are close to one or more of them. It is probably unwise to attempt any taxonomic subdivision of *Argemone* above the rank of species.

Species Concept

In delimiting the species of *Argemone,* I have been guided by the following generalizations. When two taxa are sympatric over a part of their ranges and evidence indicates that they hybridize readily in this area they are generally treated as subspecies of the same species. If there is no visual evidence of hybridization between the two taxa they are treated as distinct species. When the ranges of two taxa are allopatric but experience with greenhouse cultures indicates that they may be crossed readily and produce rather highly fertile offspring they are also generally treated as subspecies of the same species. If two taxa occupy allopatric ranges and consequently are effectively isolated spatially and, further, if their crossability is unknown, then they are treated as distinct species.

Differences in ploidy level between individuals of different breeding populations or of those within a single population have not been considered to be of nomenclatorial relevance unless accompanied by morphological differentiation. Such differences in ploidy level may obviously be of great biological significance in their effects on the breeding behavior and evolution of the species. It happens, however, that in *Argemone* the ploidy level is constant in most species insofar as has been determined; conversely, differences in ploidy level are generally accompanied by morphological differentiation of sufficient magnitude to warrant a degree of taxonomic recognition.

Speciation

The present study indicates that the most important factor leading to speciation in *Argemone* is geographic isolation followed by the accumulation of genetic differences in the isolated populations. One of the most interesting features of the genus is the manner in which one species is replaced by another geographically. In the United States, *A. polyanthemos* is replaced to the west and southwest by *A. hispida* and *A. squarrosa* subspp.

and these are replaced by *A. gracilenta*, *A. corymbosa* subspp. and *A. munita* subspp. still farther west. To the south and southeast, *A. polyanthemos* is replaced by *A. chisosensis*, *A. albiflora* subsp. *texana* followed by *A. sanguinea* and *A. aenea*. Other species occupy smaller but discrete ranges within this larger area. There is, of course, some overlapping of distributional ranges, but these are more apparent than real. This is because the two partially sympatric species occupy different ecological positions. In Mexico, similar conditions to those in the United States prevail. All of the Mexican species have partially or wholly discrete geographical ranges.

Many diploid species such as *A. albiflora* and *A. polyanthemos* appear to maintain their identities mainly because of geographic isolation. Breeding experiments indicate that these two species will cross readily under experimental conditions. *A. gracilenta*, a diploid species mainly of the Sonoran Desert, is perfectly distinct over most of its range, but appears to hybridize with *A. pleiacantha* subsp. *pleiacantha* where the latter has been introduced into its range.

Another factor which has played a role of some significance in *Argemone* speciation is polyploidy accompanied by reproductive isolation. It is postulated that *A. ochroleuca* may have arisen as an autotetraploid of *A. mexicana*. These species are very much alike in general characteristics and reproductive behavior. Plants of both species are highly self-compatible, and both species exhibit a high degree of crossability with other species. *A. mexicana* now occupies a very different geographical range from *A. ochroleuca* (see Fig. 5), and the occurrence of the former in the range of the latter may be attributed entirely to introductions. Diploid and tetraploid races herein included under *A. sanguinea* occupy slightly different though adjacent geographical areas and exhibit some inconstant morphological differences. This type of variation might easily lead to speciation. Two species which are effectively isolated from all others are *A. aurantiaca*, a hexaploid, and *A. squarrosa* subsp. *squarrosa*, probably an octaploid. These two species may be crossed with diploid and tetraploid species under experimental conditions, but the resultant highly unbalanced genomes in the F_1's lead to complete sterility of these hybrids.

The presence of sterility barriers between individual species pairs in *Argemone* are not uncommon, although the exact nature of these barriers has not been investigated. For example, *A. platyceras* has been successfully crossed with only one other species to date, namely, *A. mexicana*, but attempts to cross it with its nearest relative, *A. arida*, have not been made. Once sterility barriers have formed between segments of a population, even though they are not complete, the potentiality for genetic drift, either morphological or in the direction of different ecological amplitudes (i.e.,

differing habitat optima), or more likely both, may lead to speciation. Probably this factor is involved in speciation within the genus *Argemone*. It is unlikely, however, that sterility barriers have played the primary role.

Hybridization

Well authenticated instances of natural hybridization in *Argemone* are not numerous. This is partly due to lack of opportunity for hybridization since over most of the geographical range of the genus the species are spatially or ecologically isolated from each other. Well authenticated instances of putative natural hybridization, however, do occur, the best example between *A. munita* subsp. *munita* and *A. munita* subsp. *rotundata* in southern California in a small area of sympatric distribution where hybrid swarms of the two are common. Curiously enough, plants of intermediate character occur far up the coastal ranges where neither subspecies is found in typical state. This is the main basis for placing these two taxa in the same species, the two being otherwise sufficiently distinct and separated geographically to justify treating them as separate species. In Sonora, single hybrid plants of *A. pleiacantha* subsp. *pleiacantha* X *A. ochroleuca* subsp. *ochroleuca* are not uncommon, but these always appear to be F_1 hybrids which do not reproduce. The latter species is almost certainly introduced into the area where the hybrids occur. *A. gracilenta* appears to hybridize with *A. pleiacantha* subsp. *pleiacantha* and *A. pleiacantha* subsp. *ambigua* in southern and western Arizona in and near the areas of distributional overlap. *A. polyanthemos* and *A. albiflora* subsp. *texana* seem to hybridize freely in north-central Texas. In southern Texas several introduced and native argemones are found in more or less close proximity. The variation patterns of such species as *A. sanguinea* (diploid and tetraploid) and *A. albiflora* subsp. *texana* (diploid) in this area are not understood; part of this variation may be due to genetic interchange between these and other species. Further studies on the southern Texas argemones are much needed.

The classical work on controlled interspecific hybridization in *Argemone* is that of Vilmorin (1912). Vilmorin succeeded in crossing *A. mexicana* and *A. platyceras* and in growing first and second generation progeny. From the distribution given for *A. platyceras*, i.e., Rocky Mountains: Wyoming, Nebraska, Texas, one might suspect that Vilmorin's *A. platyceras* was actually *A. polyanthemos*. For reasons clarified below, I am of the opinion that he was working with true *A. platyceras* from Mexico. Vilmorin reported segregation in the F_2 for flower size and color, stem color, latex color, stature, abundance of foliage, color of the nerves, etc. Monstrosities resulting from malformations of the floral organs were also

reported, e.g., stamens transformed into carpels. Most important, he reported that some F_2 plants had flowers with petals of varying shades of buff. Since one parent had bright yellow petals and the other white, recombinations giving a new color are of extraordinary interest.

I have repeated Vilmorin's experiments exactly with parental stocks of known origin and have obtained identical results. I have, unfortunately, been unable to grow large populations of F_2 plants, having succeeded in rearing to maturity a total of only 36 plants. Only one plant had "buff" (actually bronze-colored) petals and, interestingly, this plant was identical to *A. aenea* of Texas and northeastern Mexico. This experiment should be repeated for absolute confirmation with large populations, and, if *A. aenea*-like progeny are recovered, a further step should be taken, that is, selection in succeeding generations with a view to reconstituting *A. aenea*. I am not at all sure that this cross is the one actually involved in the evolution of *A. aenea*, although *A. mexicana* is almost certainly one of the parents. The other parent is more likely a lavender-flowered, diploid race of *A. sanguinea*. The bronze color of the petals in *A. aenea* is possibly resultant from the presence of both purple and yellow pigments. Although lavender filaments are generally present in *A. platyceras*, the coloration does not carry over to the petals in-so-far as is known.

Numerous other attempts at controlled crossing of *Argemone* species have been made by the writer in the greenhouses at the University of Minnesota. The species most often involved in these crosses have been *A. mexicana*, *A. ochroleuca* subsp. *ochroleuca*, *A. platyceras*, *A. polyanthemos*, *A. albiflora* subspp., *A. aenea*, *A. grandiflora* subspp., and *A. sanguinea*. Publication of details of these experiments must be deferred to a later date, but some generalities may be mentioned here. Experimental hybridization between many species of *Argemone* is possible, and no species seems to be completely isolated from all other species by sterility barriers. *A. platyceras* is most nearly isolated; crosses of this species were successful only with *A. mexicana* among several species tried. *A. mexicana* and *A. ochroleuca* can be successfully hybridized with most if not all other species. Interspecific crosses can be carried beyond the first generation only if the ploidy levels of the parental species are the same. Numerous first and second hybrid generation populations were grown in the experimental gardens of the University of Minnesota and the Rancho Santa Ana Botanic Gardens. In general, a marked loss in vigor and fertility in F_2 plants was evident. This indicates the prevalence of incompatible genomes in *Argemone* species even among those which are crossable under experimental conditions.

Chromosome Numbers

Chromosome numbers have been determined for the species listed in the table below. Root tip sections have been employed in making most of these counts. In *A. corymbosa*, *A. gracilenta*, *A. munita* and *A. pleiacantha* the counts have been made from PMC squashes.

It is evident from the table that most species of *Argemone* have a somatic chromosome number of 28. The polyploids form a nearly regular series with known somatic chromosome number of 56 (4 species), 84 (1 species) and ca. 112 (1 species). A meiotic number of 14 is recorded for two putative hybrids between *A. ochroleuca* and *A. pleicantha*. This is at variance with the expected situation in an F_1 cross between these two species, the former a tetraploid, the latter a diploid. Herein lies indirect evidence that *A. ochroleuca* may sometimes have a somatic chromosome number of 28. Pairing of the chromosomes at Metaphase-I was nearly regular in the hybrids.

The chromosome counts listed below have all been made by myself over a period of several years. The only other counts for this genus known to me are those reported by Sugiura. Sugiura (1936, p. 570) reports the meiotic number for *A. grandiflora* as 28 and that for *A. mexicana* as 14. These counts are in agreement with my own studies. Sugiura (1940, p. 564) further reports the meiotic number for *A. barclayana* as 14. I do not know which species is referred to by this name, since in my opinion the binomial falls into synonomy under *A. ochroleuca* subsp. *ochroleuca*, a tetraploid with 56 somatic chromosomes over most of its range, with the possible reservation noted above. I agree with Sugiura (1940) that the basic chromosome number in the genus may be 7, but it now appears doubtful if any species with a meiotic number of 7 survive.

General Morphology

Roots: Seedlings of *Argemone* initially produce a strong tap root in all species observed. In certain species such as *A. polyanthemos*, when growing in sandy soil, the tap root may penetrate to a depth of two or more feet. In other species large lateral roots soon develop and the root system is consequently more diversified.

Stems: In all of the herbaceous species of *Argemone* the young plants first produce a basal rosette of leaves. A main stem then arises from the apex and often one or more additional stems arise concurrently from axillary buds near the base of the plant. Often, however, the axillary buds do not become active until after growth of the central stem has ceased and may even be delayed until the advent of the next growing season.

TABLE I

Species	Collector and number	Locality where collected	Garden number	n	2n
A. acnea	*G. B. Ownbey & F. Ownbey 1409*	17.5 mi. n.w. of Montemorelos, Nuevo Leon, Mexico	A-50- 2 A-50- 5		28
	F. G. Meyer & D. J. Rogers 2479	54 mi. s. of Matamoros, Tamaulipas, Mexico	A-12- 1		28
A. albiflora subsp. *albiflora*	*G. B. Ownbey & F. Ownbey 1350*	Savannah, Chatham Co., Georgia	A-35- 5		28
	G. B. Ownbey & F. Ownbey 1375	Carrabelle, Franklin Co., Florida	A-37- 2 A-37- 5		28
	G. B. Ownbey & F. Ownbey 1379	4.5 mi. e. of Gulfport, Harrison Co., Miss.	A-39- 2 A-39- 3		28
A. albiflora subsp. *texana*	*C. B. Heiser s.n.*	Brazos River, Hwy. 21, Burleson Co., Texas	A-24- 1		28
	C. B. Heiser s.n.	Athens, Henderson Co., Texas	A-25- 1		29
	G. B. Ownbey & F. Ownbey 1387	4.3 mi. e. of Hempstead, Waller Co., Texas	A-43- 1 A-43- 4		28
A. arida	*G. B. Ownbey & F. Ownbey 1444*	1.6 mi. s.e. of Nombre de Dios, Durango, Mexico	A-59- 4		28
	B. G. Ownbey & F. Ownbey 1447	6.3 mi. n.e. of Villa Madero, Durango, Mexico	A-60- 1 A-60- 2		56
A. aurantiaca	*C. B. Heiser s.n.*	Selma, Bexar Co., Texas	A-21- 2 A-22- 1 A-22- 4		84
	G. B. Ownbey & F. Ownbey 1394a	5.3 mi. s.e. of Austin, Travis Co., Texas	A-44- 1 A-44- 5		84
A. corymbosa subsp. *arenicola*	*G. B. Ownbey & F. Ownbey 2146*	37.9 mi. s.w. of Green River, Emery Co., Utah		28	
	G. B. Ownbey & F. Ownbey 2164	21.8 mi. s.w. of Bluff, San Juan Co., Utah		28	
A. echinata	*G. B. Ownbey & F. Ownbey 1408*	2.1 mi. n. of Saltillo, Coahuila, Mexico	A-49- 1 A-49- 9		28
A. gracilenta	*G. B. Ownbey & F. Ownbey 2079*	2.2 mi. s. of Villa de Seris, Sonora, Mexico		14	
	G. B. Ownbey & F. Ownbey 2079a	3.7 mi. s. of Villa de Seris, Sonora, Mexico		14	
A. grandiflora subsp. *armata*	*F. G. Meyer & D. J. Rogers 2836, in part*	Hacienda Santa Engracia, 40 mi. n.w. of Victoria, Tamaulipas	A-13- 6 A-13-10		56
	G. B. Ownbey & F. Ownbey 1406	Santa Catarina, Nenvo León, Mexico	A-48- 2		56

TABLE I (continued)

Species	Collector and number	Locality where collected	Garden number	n	2n
A. grandiflora subsp. *grandiflora*	*R. Straw M18*	El Pinalito, Hidalgo, Mexico	A-3 - 5		56
	R. Straw M61, M62	ca. 6 mi. e. of Ciudad del Maíz, San Luis Potosí, Mexico	A-8 - 1 A-9 - 3		56
	G. B. Ownbey & F. Ownbey 1420	30.4 mi. s. of Jacala, Hidalgo, Mexico	A-52- 1 A-52- 5		56
A. mexicana	*F. G. Meyer & D. J. Rogers 2677, in part*	8 mi. e. of Dulces Nombres, Nuevo León or Tamaulipas, Mexico	A-11- 3 A-11- 5		28
	Cultivated, Univ. Minnesota	Origin unknown	A-16- 1		28
	G. B. Ownbey & F. Ownbey 1357	St. Augustine, St. John's Co., Florida	A-40- 3 A-40- 5		28
	G. B. Ownbey & F. Ownbey 1366	South Miami, Dade Co., Florida	A-41- 2 A-41- 4		28
A. munita subsp. *argentea*	*G. B. Ownbey & F. Ownbey 2113*	Beal Well, Imperial Co., California		14	
A. munita subsp. *munita*	*G. B. Ownbey & F. Ownbey 2112*	2.8 mi. s.e. of Palm Springs, Riverside Co., California		14	
	G. B. Ownbey & F. Ownbey 2171	1.6 mi. s.w. of Emory store, San Diego Co., California		14	
A. munita subsp. *robusta*	*G. B. Ownbey & F. Ownbey 2177*	Santiago Peak, Orange Co., California		14	
A. munita subsp. *rotundata*	*G. B. Ownbey & F. Ownbey 2168*	2.0 mi. w. of Cajon Junction, San Bernardino Co., California		14	
A. munita subsp. *munita* X subsp. *rotundata*	*B. G. Ownbey & F. Ownbey 2170*	0.1 mi. w. of Radec, Riverside Co., California		14	
A. ochroleuca subsp. *ochroleuca*	*F. G. Meyer & D. J. Rogers 2677, in part*	8 mi. e. of Dulces Nombres, Nuevo León or Tamaulipas, Mexico	A-11- 1 A-11- 4		56
	G. B. Ownbey & F. Ownbey 1421	7.9 mi. n. of Tasquillo, Hidalgo, Mexico	A-53- 1 A-53- 2		56
	G. B. Ownbey & F. Ownbey 1443	17.1 mi. n.w. of Sombrerete, Zacatecas, Mexico	A-58- 4		56
	G. B. Ownbey & F. Ownbey 1460	3.5 mi. s.e. of Meoqui, Chihuahua, Mexico	A-63- 2 A-63- 5		56
A. ochroleuca subsp. *ochroleuca* X *A. pleiacantha* subsp. *pleiacantha*	*G. B. Ownbey & F. Ownbey 2078*	3.6 mi. n. of Imuris, Sonora, Mexico		14	

TABLE I (continued)

Species	Collector and number	Locality where collected	Garden number	n	2n
	G. B. Ownbey & F. Ownbey 2088	3.1 mi. n.e. of Santa Ana, Sonora, Mexico		14	
A. platyceras	*R. Straw M33*	ca. 12 mi. s.e. of Puebla, Puebla, Mexico	A-4 - 5		28
	R. Straw M38	1.1 mi. w. of Puebla, Puebla, Mexico	A-5 - 3		28
	R. Straw M39	ca. km. 114 w. of Mexico City, Mexico	A-6 - 1 A-6 - 2		28
	R. Straw M40	near San Juan Paracutín, Michoacan, Mexico	A-7 - 1 A-7 - 2		28
A. pleiacantha subsp. *pleiacantha*	*G. B. Ownbey & F. Ownbey 2077*	15.2 mi. s. of Nogales, Sonora, Mexico		14	
A. polyanthemos	*E. Anderson s.n.*	30 mi. e. of Amarillo, Carson Co., Texas	A-20- 3		28
	G. B. Ownbey & F. Ownbey 1298	25.2 mi. s. of Custer, Custer Co., S. Dokata	A-26- 2		28
	G. B. Ownbey & F. Ownbey 1323	7.9 mi. n.w. of Gothenburg, Lincoln Co., Nebraska	A-30- 4 A-30- 5		28
A. sanguinea	*V. L. Cory 55221*	4¾ mi. e. of Falfurrias, Brooks Co., Texas	A-19- 3		56
	B. E. Harrell 152	9 mi. s.e. of Laredo, Webb Co., Texas	A-18		28
	C. B. Heiser s.n.	Carrizo Springs, Dimmit Co., Texas	A-23- 1 A-23- 2		28
	G. B. Ownbey & F. Ownbey 1451	57.3 mi. w. of Gómez Palacio on road to Mapimí, Durango, Mexico	A-71- 1 A-71- 2		ca. 58
A. squarrosa subsp. *squarrosa*	*G. B. Ownbey & F. Ownbey 1477*	0.6 mi. s.w. of Capitan, Lincoln Co., New Mexico	A-67- 1 A-67- 2		ca. 112

Branching of the stem of *Argemone* is sympodial, i.e., growth of each primary, secondary, tertiary, etc., axis is in turn arrested by the formation of a terminal flower bud. It is usual for the axillary shoot or shoots nearest the primary flower bud of each axis also to produce terminal flower buds immediately. The branch system develops concurrently in its various parts, but the sequence of maturation of flowers and fruits in each part of the system is always the same, the terminal flower or fruit of each axis being the most advanced.

In many cases the inflorescence of *Argemone* is clearly a cyme as delimited by Rickett (1955); in other cases, although it is structurally identical, it fits this definition of a cyme less well since through overtopping of

the main axes by the lateral axes the flat topped character is lost. In these cases, which are numerous, the inflorescence could as well be termed a panicle in Rickett's proposed usage for the term.

With rare exceptions, viz., in *A. grandiflora* and *A. mexicana* f. *leiocarpa*, the stems of *Argemone* are always prickly to a greater or lesser extent. The amount of prickliness varies within wide limits between species and sometimes within a single species. The amount of prickliness is of considerable diagnostic importance, but is extremely hard to express descriptively. A better idea of this characteristic in a given species may be gained by the reader from the illustrations.

Leaves: The leaves of *Argemone* must be considered to be epetiolate since a clearly defined petiole is not present. In the lowermost leaves, which are obovate or oblanceolate, the blade becomes quite narrow near its point of attachment and, in a sense, might be considered to have a winged petiole. The middle and upper cauline leaves are definitely sessile and elliptical to sometimes ovate. Those of the uppermost extremities of the stem, in most species, are much reduced and bracteate.

The leaf blades, beyond the seedling growth stages, are always lobed to some extent except, insofar as is known, in *A. subintegriofolia*. On a given plant the lower cauline leaves, but not necessarily those of the basal rosette, are the most deeply lobed. The leaves are regularly less deeply lobed and reduced in size upward.

The margins of the leaves are invariably toothed, sometimes closely so. Each tooth, regardless of its size, is always terminated by a prickle.

The surfaces of the leaves range from smooth to closely prickly or crisped-hispid. The prickles are confined to the main veins in many species but, as the amount of prickliness increases, they also occur on the lesser veins and on the intervein areas in extreme cases.

Buds: The buds of *Argemone* vary greatly in shape just prior to anthesis, from subspherical to elliptical, oblong, or obovate. The sepals normally are three in number, but the number may vary from two to six and is not necessarily constant on a single plant. They are fugacious and deciduous at anthesis. Each sepal has a hollow, subterminal horn tipped by a solid prickle. The length and shape of the sepal horns is of some diagnostic value. The sepals in the bud are imbricated. The overlapped portion is of thinner, more delicate texture and is regularly prolonged into an acute or obtuse tooth at the distal end. The petals, which reach their full size just before anthesis, are crumpled in the bud upon release from the confinement imposed by the sepals at anthesis rapidly assume their mature shape.

Flowers: The flowers when fully opened are saucer-shaped or bowl-shaped. Normally there are six petals in two whorls of three each. The

individual petals are narrowly elliptical in *A. ochroleuca* subsp. *stenopetala* to approximately obcuneate in *A. ochroleuca* subsp. *ochroleuca* and *A. platyceras*. They are obovate or suborbicular in *A. albiflora*, *A. munita* and *A. gracilenta* as well as many other species. In a single flower, the petals of the outer whorl tend to be broader and more rounded distally than the petals of the inner whorl. The floral anatomy of *Argemone* and other papaveraceous genera is discussed by Murbeck (1912).

Stamens: the stamens in *Argemone* are numerous, but the number for each species usually falls within roughly definable limits. They occur in an indefinite number of series. The extrorse anthers are linear, 2-celled and dehiscent along their entire length. The filaments are thread-like (narrowly elavate in *A. glauca* of the Hawaiian Islands), basifixed and abruptly contracted at the point of attachment to the anther.

Pistils: The pistil consists of a 3-7-lobed stigma, a short or obsolete style, and a 3-7-carpellate ovary with as many placentae. The felt-like stigma is lobed by virtue of the down-warping and expansion of the stigmatic surfaces opposite the placental strands. The lobes formed by the down-warped stigmatic tissue are distally concave and more or less tubular proximally. The style consists mainly, if not entirely, of the fused placental strands. It is solid at anthesis but a slender central channel may develop later. Free but very limited passage of air to and from the interior of the ovary is then possible. The ovary is unilocular with parietal placentation. The anatropous ovules are numerous and uniformly oriented with the micropyle pointed towards the base of the ovary. The medial plane of each ovule is at right angles to the surface of the placenta insofar as space permits. The raphe is conspicuously umbonate at the chalazal end in the species observed.

Capsules: The capsules at maturity vary greatly in shape, from narrowly elliptical to oblong, lanceolate or ovate. The surface is always spinescent to a greater or lesser degree except in *A. mexicana* f. *leiocarpa*. There are 3-7 carpels; each carpel consists of a broad reticulate-veined valve which it attached along the margins to an adjacent vascular strand underlying a placenta. At maturity the valves break away apically from the associated vascular strands for about one-third of their length. The exposed strands remain in place and form a cage-like framework which terminates in the persistent stigma and style. The seeds are dispersed, often over long periods of time, through the openings between the strands.

Seeds: The seeds of *Argemone* are subspherical or slightly tapered towards the micropyle. A slender but often prominent beak is formed at the micropyle. The hilum is small and often obscure. The raphe is straight and often definitely umbonate at the chalazal end. The testa is described in all the older literature as being scrobiculate and I have found no better

term. Shallow depressions cover the entire surface. The depressions are arranged in more or less definite longitudinal rows between the chalaza and the micropyle. The ones farthest from the raphe are the most pronounced; those nearest the raphe are the least pronounced. The greatest dimension of the seed varies from 1-3 mm. The size range within a species is sufficiently narrow to be of taxonomic value. The diameters of the depressions in the testa vary in direct proportion to the sizes of the seeds and, as a consequence, this feature has proved to be of little taxonomic use.

Seedlings: Upon germination of the seed a deep tap root is rapidly developed; its ultimate length is at least in part controlled by the type of soil and availability of moisture in the surface layers. The cotyledons are linear and entire. The first few leaves are unlobed but are obtusely angled marginally. Later leaves are progressively dentate, lobed or even pinnatifid, depending on the species, until the adult leaf forms appear.

Other Features of Taxonomic Value

Longevity: In all species of *Argemone* with the possible exception of *A. fruticosa* the plants probably are capable of completing their life cycle in a single growing season. Plants of many species are capable of perennating by means of the persistent root and crown and the activation of latent, sub-basal axillary buds when conditions are favorable. Life span of the individual plants thus sometimes may be of taxonomic value.

Petal color: As a whole, the color of the petals in *Argemone* exhibit considerable variation, although the prevailing color is white. Many individual plants of *A. sanguinea* and *A. chisosensis* have petals of pale to dark lavender, but white petals often are present in both species. Several species have petals which are of yellow color, for example, *A. mexicana*, *A. ochroleuca* and *A. fruticosa*. Flowers of a single plant have a uniform color of petals in all instances. The petals remain attached for a comparatively short time, usually for no more than two or three days.

Latex color: Abundant latex is present throughout the plant in all species of *Argemone*. According to Metcalfe and Chalk (1950), the latex is reported to be contained in articulated laticiferous tubes in this genus. Whether or not its occurrence is restricted to these tubes or is sometimes found in laticiferous sacs as in some other papaveraceous genera evidently is not known. The amount of "bleeding" of a freshly broken stem is often considerable. This would lead one to believe, therefore, that the latex is generally if not universally present in tubes and that there is drainage to the break from some distance up and down the stem. The latex, when fresh, varies greatly in color and this feature often is of diagnostic importance. In such species as *A. hispida*, *A. gracilenta* and *A. munita* it is

generally very pale lemon-yellow; in other species, for example, *A. mexicana*, *A. ochroleuca* and *A. polyanthemos* it is generally bright yellow. In *A. corymbosa* the latex is distinctly orange and in *A. aurantiaca* it is consistently reddish-orange. Upon drying, the latex of all species turns to a deep brownish-black color.

Acknowledgments

I am very grateful to the curators of the various herbaria who have generously placed the specimens at their institutions at my disposal. I wish to extend my most sincere thanks to Dr. Philip A. Munz for opening the facilities of the Rancho Santa Ana Botanic Garden to my use during the first six months of 1953 and for much other assistance freely given during this period. I have had free access to the herbarium and library of the Missouri Botanical Garden on numerous occasions through the courtesy of Dr. Edgar Anderson who has also helped me in many other ways. Many persons have sent me seeds of various *Argemone* species, namely Drs. E. Anderson, C. B. Heiser, F. G. Meyer, Teodoro Meyer, L. H. Shinners, Richard Straw, W. A. Weber, and Mr. V. L. Cory. I am most grateful to all these colleagues. Bibliographic and geographic information has been generously supplied by Drs. W. M. Benner, R. C. Foster, C. L. Porter, W. B. Turrill, and Mr. J. R. Swallen. Miss Nell C. Horner has been of invaluable service in preparing the Latin descriptions. All of the illustrations are the results of the dedicated efforts of Miss Wilma Monserud. Dr. L. C. Hulbert has carried out useful tests on means of breaking the dormancy of *Argemone* seeds. My colleagues in the Department of Botany, University of Minnesota, especially Dr. T. Morley, have discussed special aspects of these investigations with me on countless occasions. Finally, the indefatigable efforts of my wife, Marion Findley Ownbey, on our numerous field trips have contributed much to the success of these ventures.

Financial support for these investigations has been supplied by the Graduate School of the University of Minnesota for the past several years. The writer was also appointed to a Fellowship by the Guggenheim Foundation for 1952-1953. This appointment made possible extensive field and garden studies which would not have been otherwise possible.

Herbarium Abbreviations

The herbarium abbreviations used in this paper are in accord with those listed by Lanjouw and Stafleu (1954). Specimens from the following herbaria have been consulted during the course of this study:

C. . . . . Botanical Museum and Herbarium, University of Copenhagen.
CAS. . . . . Herbarium of the California Academy of Sciences.
DAV. . . . . Herbarium of the University of California, Davis.
DS. . . . . Dudley Herbarium, Stanford University.
F. . . . . Herbarium of the Chicago Natural History Museum.
GH. . . . . Gray Herbarium, Harvard University.
K. . . . . The Herbarium and Library, Royal Botanic Gardens, Kew.
KANU. . . . . Herbarium of the University of Kansas.
KSC. . . . . Herbarium of Kansas State College of Agriculture and Applied Science.
MEXU. . . . . Herbario Nacional del Instituto de Biologia, Universidad Nacional de México.
MIN. . . . . Herbarium of the University of Minnesota.
MO. . . . . Herbarium of the Missouri Botanical Garden.
ND. . . . . Herbarium of the University of Notre Dame, Indiana.
NEW MEX. . . Herbarium of the University of New Mexico (no standardized abbreviation assigned).
NY. . . . . Herbarium of The New York Botanical Garden.
PH. . . . . Herbarium of the Academy of Natural Sciences, Philadelphia.
POM. . . . . Herbarium of Pomona College.
RM. . . . . Rocky Mountain Herbarium, University of Wyoming.
RSA. . . . . Herbarium of the Rancho Santa Ana Botanic Garden.
SMU. . . . . Herbarium of Southern Methodist University.
TEX. . . . . Herbarium of the University of Texas.
UC. . . . . Herbarium of the University of California, Berkeley.
US. . . . . Herbarium of the United States National Museum.

Systematic Treatment

Argemone L., Sp. Pl. 1: 508-509. 1753,

excluding *A. armeniaca* and *A. pyrenaica* (from the Greek αργεμα, the cataract of the eye for which the juice of a poppy-like plant of the same name was a supposed remedy); [Tournef., Elem., p. 204, t. 121. 1694; Inst. Rei Herb. 1: 239, 2: t. 121. 1700]; L., Gen. Pl., ed. 5, p. 225. 1754; Lamarck, Encycl. Meth. 1: 247. 1783; Gaertn., Fruct. et Sem. Pl. 1: 287, t. 60. 1788; Jussieu, Gen. Pl., p. 236. 1789; Lamarck, Planches 2: t. 452. 1797; Tornef., Elem., ed. aug. (Jolyclerc) 2: 12, 5: t. 121. 1797; Nutt., Gen. 2:9. 1818; DC., Reg. Veg. Syst. Nat. 2: 85. 1821; DC., Prodr. 1: 120. 1824; Bernh., in Linnaea 8: 461. 1833; Endl., Gen Pl., p. 856. 1836-1840; Meisner, Pl. Vasc. Gen., pars prior, p. 7, pars altera, p. 9. 1836-1843; Gray, Gen. Pl. U. S. 1: 111, t. 47. 1849; Benth. & Hook., Gen. 1 (1): 52. 1862; Baillon, Hist. Pl. 3: 112-113, figs. 125-127. 1871; Prantl & Kündig, in Engler & Prantl, Nat. Pflanzenf. 3 (2): 141. 1889; Prain, in Journ. Bot. 33: 129. 1895; Gray, Syn. Fl. N. Am. 1 (1): 87-88. 1895; Rose, in Contrib. U. S. Nat. Herb. 8: 23-27. 1903; Fedde, in Engler, Pflanzenr. 4 (104): 271. 1909.

Ectrus Lour., Fl. Cochinch. 1: 344. 1790.

Enomegra Nels., Analyt. Key Fl. Pl. Rocky Mt. Reg., p. 27. 1902; Nels., in Bot. Gaz. 34: 365. 1902.

Annual or perennial herbs (one shrub) with a persistent or ephemeral tap root. Latex pale lemon-yellow, almost white, through various shades of yellow to bright golden yellow, orange, or reddish-orange. Stems glaucous, 1-10 (-25 or more), erect or ascending, 2-10 (-20) dm. tall, each axis determinate, essentially smooth to closely prickly. Leaves glaucous, apetiolate, those of the basal rosette and lower stem obovate to oblanceolate, the middle and upper cauline progressively elliptical or ovate, the upper ones often clasping, the ultimate foliar organs very much reduced and bracteate. Leaf margins always dentate, each tooth terminated by a prickle, the blade otherwise wholly unlobed or, commonly, shallowly to deeply lobed. Leaf surfaces essentially smooth to closely prickly, hispid, or crisped-hispid, the areas over the main veins often of a lighter

bluish cast and thereby contrasting with the deeper bluish coloration of the remaining intervein surfaces. Flower buds narrowly to broadly oblong, obovate, elliptical or subspherical. Sepals caducous, normally 3 (2-6), imbricated, essentially smooth to variously prickly and hispid, each with a subterminal horn. Sepal horns hollow and herbaceous basally, terminated by an indurated prickle, terete or variously angular or flattened in cross-section. Flowers 3-15 cm. in diameter when fully expanded, either closely subtended by or separated by 1-several mm. from the nearest foliar bract. Petals normally 6, in two whorls of 3, narrowly elliptical to obcuneate, obovate or suborbicular, the outer margin minutely erose, in color, of various shades of yellow, or golden, bronze, lavender, or white. Stamens about 20-250 or more per flower, and filaments filiform, rarely clavate, usually pale lemon-yellow, but occasionally red to lavender, the anthers linear, basifixed, 2-celled, with longitudinal, extrorse dehiscence, coiled after anthesis, bright yellow or occasionally purplish. Stigma 3-5 (-7) -lobed, the lobes concave, formed by a down-folding of the stigmatic surface opposite each placentum, the receptive surfaces felt-like, purple (rarely yellowish-green). Style essentially absent or quite evident on mature capsules. Ovary unilocular, 3-5 (-7) -carpellate, with an equal number of placentae. Capsules fluted on the sutures, the valves splitting away from the vascular elements apically and for about one-third their length along the sutures, the exposed portion of the vascular elements forming a cage-like framework which remains attached at the tip to the persistent stigma, in shape, the mature unopened capsules varying from oblong to elliptical, ovate, or lanceolate, in armature varying from totally glabrous to very closely spinescent. Ovules numerous. Seeds blackish-brown, subspherical, the longest dimension 1-3 mm., anatropous, apiculate at the micropyle, the raphe straight, prominent, more or less umbonate at the chalazal end, the testa conspicuously scrobiculate under magnification, the endosperm copious, the embryo minute, straight, embedded in the endosperm.

Type species: *A. mexicana* L. The pre-Linnaean history of this species is fully discussed by Prain (1895, p. 130).

Distribution: Coastal areas of southeastern and southern United States; in the west from southern Montana and western South Dakota southward across the plains to the Gulf of Mexico, southwestward to California, Arizona and New Mexico; throughout the West Indies, Mexico and Central America; in South America in Chile, Argentina, Uruguay, Paraguay, Bolivia and northward along the coasts to the Isthmus of Panama; Hawaii; *A. mexicana* by introduction in tropical and subtropical lands around the world.

Key to the species:

1. Petals pale lemon-yellow, bright yellow, sulphur-yellow, golden or bronze.
   2. Stems woody, perennial; petals pale yellow to sulphur-yellow; southern Coahuila . . . . . 1. *A. fruticosa*
   2. Stems herbaceous, annual, the underground parts often perennial.
      3. Petals ordinarily white but sometimes with a yellowish cast.
         4. Sepal horns strongly flattened in a radial plane; flowers usually separated from the nearest subtending foliar bract by several mm.; stamens about 75; capsules elliptical to ovate-elliptic, the surface closely spinescent and prickly, the armature nearly or completely obscuring the capsular surface; Vera Cruz to Michoacán . . . . . 15. *A. platyceras*
         4. Sepal horns usually angular, sometimes flattened, but not as above; flowers usually more closely subtended by 1-2 foliar bracts; stamens 80-120 or more; capsules oblong-elliptic to lanceolate, the surface thinly to rather closely spi-

nescent and prickly, the capsular surface clearly visible to partly obscured by the armature; southern Chihuahua to San Luis Potosí . . . . . 16. *A. arida*

3. Petals distinctly pale to bright yellow; capsules smooth or armed with large, well-spaced spines, these sometimes interspersed with a few smaller spines and prickles.
   5. Stamens about 20-75; flowers 3-7 cm. broad when fully expanded; petals pale lemon-yellow to bright yellow.
      6. Capsular surfaces smooth (f. *leiocarpa*) or spinescent; capsules oblong to broadly elliptical; buds subspherical; petals mostly bright yellow; stigmatic lobes appressed to the style at anthesis; West Indies and adjacent continental areas . . . . . 2. *A. mexicana*
      6. Capsular surface spinescent; capsules lanceolate, ovate-lanceolate or occasionally oblong-elliptic; buds oblong; petals mostly lemon-yellow; stigmatic lobes spreading, not appressed to the style at anthesis; Mexico outside the tropical areas . . . . . 3. *A. ochroleuca*
   5. Stamens about 150-250; flowers 7-12 cm. broad when fully expanded; petals bright yellow to golden or bronze.
      7. Petals bright yellow; filaments lemon-yellow; stigma at anthesis about 2.5-3.0 mm. broad, the lobes barely sinuate; southern San Luis Potosí . . . . . 4. *A. superba*
      7. Petals bright yellow to golden or bronze; filaments red or purplish; stigma at anthesis 3-6 mm. broad, the lobes usually distinctly sinuate; northeastern Mexico and adjacent Texas . . . . . 5. *A. aenea*

1. Petals white or of some shade of lavender.
   8. Petals of some shade of lavender.
      9. Uppermost leaves not clasping; lower leaves lobed to four-fifths of the distance to the midrib or more.
         10. Stems often closely prickly; capsules narrowly elliptic-lanceolate or elliptic-ovate; longest dimension of seeds 1.8-2.2 mm.; western Texas . . . . . 18. *A. chisosensis*
         10. Stems not closely prickly; capsules narrowly to broadly elliptical; longest dimension of seeds about 1.5 mm.; southern Texas and northeastern Mexico . . . . . 17. *A. sanguinea*
      9. Uppermost leaves clasping; lower leaves lobed to less than two-thirds the distance to the midrib; Great Plains . . . . . 22. *A. polyanthemos*
   8. Petals white.
      11. Petals narrowly elliptical, 5-8 mm. broad, 15-25 mm. long; stamens 20-30; northern Durango and southern Chihuahua . . . . . 3b. *A. ochroleuca* subsp. *stenopetala*
      11. Petals suborbicular to obovate or obcuneate, mostly 30-60 mm. long; stamens about 75-150 or more; cosmopolitan.
         12. Leaf surfaces prickly on the primary and secondary veins above and below and also minutely hispid or prickly, often closely so, between the veins; stems usually closely prickly.
            13. Largest capsular spines compound, i.e., with few to many smaller spines or prickles arising from the basal portion, usually 8-35 mm. long.
               14. Largest capsular spines about 15-35 mm. long; latex reddish-orange when fresh; Texas . . . . . 6. *A. aurantiaca*
               14. Largest capsular spines about 8-15 mm. long; latex pale lemon-yellow to yellow when fresh.
                  15. Lower cauline leaves lobed to about three-fourths the distance to the midrib, the apices of the lobes angular, the marginal teeth usually 3 mm. long or longer, not including the terminal prickle; flowers usually closely subtended by 1-2 foliar bracts.
                     16. Body of buds 8-10 mm. broad by 14-18 mm. long; sepal horns terete;

stamens about 100; northeastern Mexico ..... 7. *A. echinata*

16. Body of buds 15-20 mm. broad by 16-25 mm. long; sepal horns angular in cross-section; stamens 150 or more; western Kansas to New Mexico and western Texas ..... 8. *A. squarrosa*

15. Lower cauline leaves lobed to about one-half the distance to the midrib, the apices of the lobes usually definitely rounded, the marginal teeth usually less than 1 mm. long, not including the terminal prickle; flowers usually separated by an interval of several mm. from the nearest subtending foliar bract; western United States ..... 10c. *A. munita* subsp. *rotundata*

13. Largest capsular spines simple, usually 5-8 mm. long.

17. Lower cauline leaves lobed to three-fourths the distance to the midrib or or more; uppermost leaves not clasping the stem.

18. Leaf surfaces between the main veins densely and minutely crisped-hispid; sepal horns angular in cross-section; capsules ovate, closely spinescent, the armature completely or nearly completely obscuring the capsular surface, the largest spines about 5 mm. long; eastern base of the Rocky Mts., Wyoming to New Mexico ..... 9. *A. hispida*

18. Leaf surfaces between the main veins variously prickly but not densely or minutely crisped-hispid; sepal horns terete.

19. Capsules oblong to elliptical, armed with long, spreading spines intermixed with smaller spines and prickles, the surface greatly obscured, the largest spines 9-11 mm. long; sepal horns about 10 mm. long; stamens about 100; northeastern Mexico ..... 7. *A. echinata*

19. Capsules narrowly elliptic-lanceolate, armed with uneven-sized spines and prickles, the capsular surface clearly visible, the largest spines 5-6 mm. long; sepal horns 3-5 mm. long; stamens about 150 or more; southern Chihuahua ..... 12. *A. brevicornuta*

17. Lower cauline leaves lobed to one-half the distance to the midrib or less; uppermost leaves usually definitely clasping the stem.

20. None of the leaves lobed, the margins sometimes undulate, irregularly toothed; flowers closely subtended by 2-4 foliar bracts; longest dimension of seeds about 1 mm.; northern Baja California ..... 11. *A. subintegrifolia*

20. Lower cauline leaves usually lobed to about one-half of the distance to the midrib, the lobes usually apically rounded, toothed; flowers usually separated by several mm. from the nearest subtending foliar bract; longest dimension of seeds 1.8-2.6 mm.; western United States ..... 10. *A. munita* subspp.

12. Leaf surfaces prickly almost exclusively on the primary and secondary veins above and below, sometimes essentially smooth; stems usually with more widely spaced prickles or almost smooth.

21. Largest capsular spines compound, i.e., with few to many smaller spines or prickles arising from the basal portion, usually 8-35 mm. long.

22. Largest capsular spines 15-35 mm. long, always definitely compound; latex reddish-orange when fresh; Texas ..... 6. *A. aurantiaca*

22. Largest capsular spines 8-15 mm. long, sometimes not clearly compound; latex pale lemon-yellow to yellow when fresh; western Texas and southeastern New Mexico ..... 8b. *A. squarrosa* subsp. *glabrata*

21. Largest capsular spines simple, 4-10 (-12) mm. long.

23. Prickles of sepals and, when present, those of the sepal horns perpendicular; lower cauline leaves mostly lobed to four-fifths or more of the distance to the midrib.

24. Uppermost leaves usually definitely clasping; lower cauline leaves lobed to less than one-half, or sometimes to about three-fourths, of the distance to the midrib.

25. Lower cauline leaves lobed to about three-fourths of the distance to the midrib, the apical margins of the lobes angular, i.e., the marginal teeth prominent; latex bright yellow when fresh; central Arizona ..... 14c. *A. pleiacantha* subsp. *ambigua*

25. Lower cauline leaves lobed to one-half the distance to the midrib or less, the apical margins of the lobes tending to be rounded, i.e., the marginal teeth very short; latex pale lemon-yellow when fresh; southern California to Baja California ..... 10. *A. munita* subspp. –

24. Uppermost leaves not definitely clasping; lower cauline leaves lobed to four-fifths of the distance to the midrib or more.

26. Buds subspherical; sepal horns terete, 3-5 mm. long; capsules narrowly elliptic-lanceolate, 8-10 mm. broad exclusive of armature; latex bright yellow when fresh; southern Chihuahua 12. *A. brevicornuta*

26. Buds oblong to obovate or elliptical, rarely subspherical; sepal horns terete or flattened or angular in cross-section, 5-14 mm. long; capsules ovate to elliptical or elliptic-oblong, rarely elliptic-lanceolate, 8-18 mm. broad exclusive of armature; latex pale lemon-yellow to bright yellow when fresh.

27. Buds usually subspherical; sepal horns terete, usually slender, 8-12 (5-14) mm. long, smooth; stems armed with usually very long, scattered, perpendicular prickles; latex usually pale lemon-yellow when fresh; western Arizona, Sonora and Baja California del Sur ..... 20. *A. gracilenta*

27. Buds oblong to obovate or elliptical, rarely subspherical; sepal horns terete or flattened or angular in cross-section, various in length, nearly always prickly; stems sparsely to closely prickly; latex pale lemon-yellow to bright yellow when fresh.

28. Stems copiously long-prickly, often decumbent, diffusely branched; leaves deeply and distantly lobed to near the midrib, the narrow lobes often 5 or more times as long as broad; sepal horns terete, 12-15 mm. long; capsules 3-carpellate, narrowly elliptic-oblong, closely spinescent, the largest spines 8-10 mm. long; latex pale lemon-yellow when fresh; Grand Canyon, Arizona ..... 13. *A. arizonica*

28. Stems sparsely to copiously prickly, erect, not diffusely branched; leaves often deeply lobed, but the lobes seldom so long in proportion to their breadth as above; sepal horns terete or flattened or angular in cross-section, 5-12 mm. long; capsules 3-4 (-6) carpellate, elliptical to ovate or lanceolate, variously spinescent, the longest spines 4-8 (-10) mm. long; latex usually bright yellow when fresh.

29. Buds broadly elliptical to elliptic-oblong; sepal horns terete or angular in cross-section; petals white or some shade of lavender; capsules 3-6-carpellate, armed with larger spines intermixed with smaller spines and prickles, the largest spines 5-10 mm. long, the capsular surface clearly visible through the armature.

30. Stems often closely prickly; capsules narrowly elliptic-ovate; longest dimension of seeds 1.8-2.2 mm.; western Texas ..... 18. *A. chisosensis*

30. Stems not closely prickly; capsules narrowly to broadly elliptical; longest dimension of seeds about 1.5 mm.; southern Texas to northeastern Mexico ..... 17. *A. sanguinea*

29. Buds usually obovate, rarely subspherical or oblong-obovate; sepal horns usually flattened on the adaxial side, rarely terete; petals white; capsules 3-4-carpellate, either densely spinescent

with uneven-sized spines and prickles, the capsular surface much obscured by the armature, or to rather sparsely armed with more even-sized spines, the capsular surface clearly visible through the armature; southwestern New Mexico to Arizona and adjacent Mexico ..... 14. *A. pleiacantha*

23. Prickles of sepals and sepal horns (when present) ascending, or sepals smooth; lower cauline leaves often lobed to less than one-half the distance to the midrib.
  31. Sepal horns strongly flattened in a radial plane; stamens about 75, the filaments pale lemon-yellow to reddish-lavender; capsules closely spinescent and prickly, the armature nearly or completely obscurng the capsular surface; Vera Cruz to Michoacán ..... 15. *A. platyceras*
  31. Sepal horns not flattened as above; stamens more numerous, the filaments pale lemon-yellow, very rarely reddish-lavender; capsular surface clearly visible through the armature, or rarely partially obscured.
    32. Stems moderately to rather closely prickly; sepal horns slightly to very definitely prickly.
      33. Lower cauline leaves lobed to one-half to three-fourths the distance to the midrib; buds oblong; sepal horns more or less angular or flattened, 7-10 (-12) mm. long; stamens usually 80-120, the filaments pale lemon-yellow to reddish-lavender; largest capsular spines about 8 mm. long, the capsular surface sometimes partially obscured by the armature; southern Chihuahua to San Luis Potosí ..... 16. *A. arida*
      33. Lower cauline leaves lobed to about four-fifths the distance to the midrib; buds subspherical; sepal horns terete, 3-5 mm. long; stamens about 150 or more, the filaments pale lemon-yellow; largest capsular spines 5-6 mm. long, the capsular surface clearly visible through the armature; southern Chihuahua ..... 12. *A. brevicornuta*
    32. Stems with scattered, sometimes long prickles to essentially smooth; sepal horns smooth or very rarely with 1-few prickles near the base.
      34. Leaves thick and coriaceous, shallowly lobed (subsp. *corymbosa*), or the lower ones deeply lobed to four-fifths of the distance to the midrib (subsp. *arenicola*); stamens usually 100-120; stigma yellowish-green or purplish; latex orange when fresh; Mohave Desert, California, and southeastern Utah to adjacent Arizona ..... 19. *A. corymbosa* subspp.
      34. Leaves often succulent, but not coriaceous, variously lobed; stamens about 150 or more; stigma purple; latex pale lemon-yellow to bright yellow when fresh.
        35. Buds obovate or oblong; sepal horns usually flattened on the adaxial side, sometimes prickly.
          36. Buds obovate; sepal horns prickly; lower cauline leaves lobed to about three-fourths the distance to the midrib, the apical margins of the lobes angular, i.e., the marginal teeth prominent; latex bright yellow when fresh; central Arizona ..... 14e. *A. pleiacantha* subsp. *ambigua*
          36. Buds oblong; sepal horns smooth; lower cauline leaves lobed to about one-half the distance to the midrib or less, the apical margins of the lobes tending to be rounded, i.e., the marginal teeth very short; latex pale lemon-yellow when fresh; Orange Co., California ..... 10a. *A. munita* subsp. *robusta*
        35. Buds usually subspherical, rarely elliptical or elliptic-oblong; sepal horns terete, seldom with 1-few prickles near the base.
          37. Uppermost cauline leaves not evidently clasping; sepal horns 8-12 (5-14) mm. long; stems armed with usually very long,

scattered, perpendicular prickles; latex usually pale lemon-yellow when fresh; western Arizona, Sonora and Baja California del Sur ..... 20. *A. gracilenta*

37. Broad bases of the uppermost cauline leaves clasping; sepal horns of various lengths; stems essentially smooth to prickly with scattered, shorter prickles; latex bright yellow when fresh.
38. Stems smooth or with a very few widely scattered prickles; leaves entirely smooth on both surfaces or with a very few prickles on the veins beneath and also rarely above; buds subspherical, almost invariably totally smooth; sepal horns 7-15 mm. long; capsules broadly oblong-elliptic, with a few stout, subequal spines, the largest of which are about 5 mm. long; Hidalgo to southern Tamaulipas ..... 21a. *A. grandiflora* subsp. *grandiflora*

38. Stems definitely prickly throughout; leaves with scattered prickles on the main veins beneath, totally smooth or with a few scattered prickles on the main veins above; buds subspherical to elliptical, with scattered or rather close-set prickles; sepal horns variable; capsules variable, the largest spines 6-12 mm. long.
39. Sepal horns 7-15 mm. long.
40. Lower cauline leaves divided to about three-fourths the distance to the midrib; uppermost leaves not conspicuously clasping; buds subspherical; capsules oblong to elliptical; southern Tamaulipas to southern Coahuila ..... 21b. *A. grandiflora* subsp. *armata*

40. Lower cauline leaves divided to about two-thirds the distance to the midrib; uppermost leaves usually very broad basally and definitely clasping; buds elliptic-oblong; capsules narrowly to broadly elliptical; Great Plains ..... 22. *A. polyanthemos*

39. Sepal horns usually 3-6 mm. long.
41. Lower cauline leaves divided to about two-thirds the distance to the midrib; buds subspherical; sepal horns 3-5 mm. long; capsules 3-7-carpellate, oblong to oblong-elliptic, the spines all rather stout, even-sized and widely-spaced; coastal areas; North Carolina to Mississippi and introduced northward ..... 23a. *A. albiflora* subsp. *albiflora*

41. Lower cauline leaves divided to about four-fifths the distance to the midrib; buds subspherical to broadly elliptical; sepal horns 4-6 (rarely -10) mm. long; capsules 3-5-carpellate, narrowly elliptical, the widely spaced large spines interspersed with uneven-sized smaller spines and prickles; eastern Texas and introduced to the northeast ..... 23b. *A. albiflora* subsp. *texana*

1. Argemone fruticosa Thurber ex Gray, in Mem. Am. Acad., n.s., 5: 306. 1853.

A. fruticosa Mueller, in Walp., Ann. 4: 170. 1857; Hemsl., Biol. Cent. Am., Bot. 1: 26. 1879; Wats., in Proc. Am. Acad. 17: 318. 1882; Hemsl., Biol. Cent. Am., Bot. 4: 4. 1886; Prain, in Journ. Bot. 33: 307. 1895; Gray, Syn. Fl. N. Am. 1 (1): 87. 1895; Rose, in Contr. U. S. Nat. Herb. 8: 24. 1903; Fedde, in Pflanzenr. 4 (104): 273, 274, fig. 36A. 1909.

Perennial shrub, the latex color unknown; stems 5-20 dm. tall, ligneous, divergently

and rigidly branched, the older portions bare of foliage, beset with persistent leaf bases forming stumps to 1 mm. or more in length, the younger portions of the stem very glaucous and often with a few scattered prickles, densely leafy; leaves thick and coriaceous, very glaucous, mostly 1.5-3.5 cm. long, oblong, each of the large acute marginal teeth terminated by a long, rigid spine, the leaf surfaces entirely smooth or with 1-3 small prickles on the veins, the veins very inconspicuous; buds subspherical, the body about 11-13 mm. broad, 13-15 mm. long, smooth or with 1-3 prickles on each sepal, the horns terete in cross-section, 8-14 mm. long including the stout terminal spine, smooth; flowers 5-10 cm. in diameter, closely subtended by 1-several little if at all reduced leaves; petals pale yellow to sulphur-yellow, broadly obovate-obcuneate; stamens numerous; stigma purple, about 2 mm. wide and 2.0-2.5 mm. high, the lobes tightly compressed to each other at flowering time, expanding and spreading apart as the ovary develops; capsules 4-6-carpellate, very broadly ovate, the width, exclusive of armature, 10-15 mm., the length, including the stigma, 14-22 mm., even-spinescent, the largest spines to about 6 mm. long, the swollen-tuberculate bases of the spines obscuring the capsular surface, the surface also sparingly prickly among the tubercles; seeds 2.0-2.2 mm. long. (Ill.: Fig. 1, 1-4; Dist.: Fig. 5.)

Lectotype: *Thurber* 844, collected at "Mountain Pass, La Peña" Coahuila, Mexico, 1852 (GH; isotypes, MO, NY). Gray, l.c., quoting Thurber says " . . . met with only in the mountain pass of La Peña, near the town of Parras." The settlement of Peña is situated on the railroad about 30 miles west of Parras. Thurber's collection is in fruit only, and is most fragmentary.

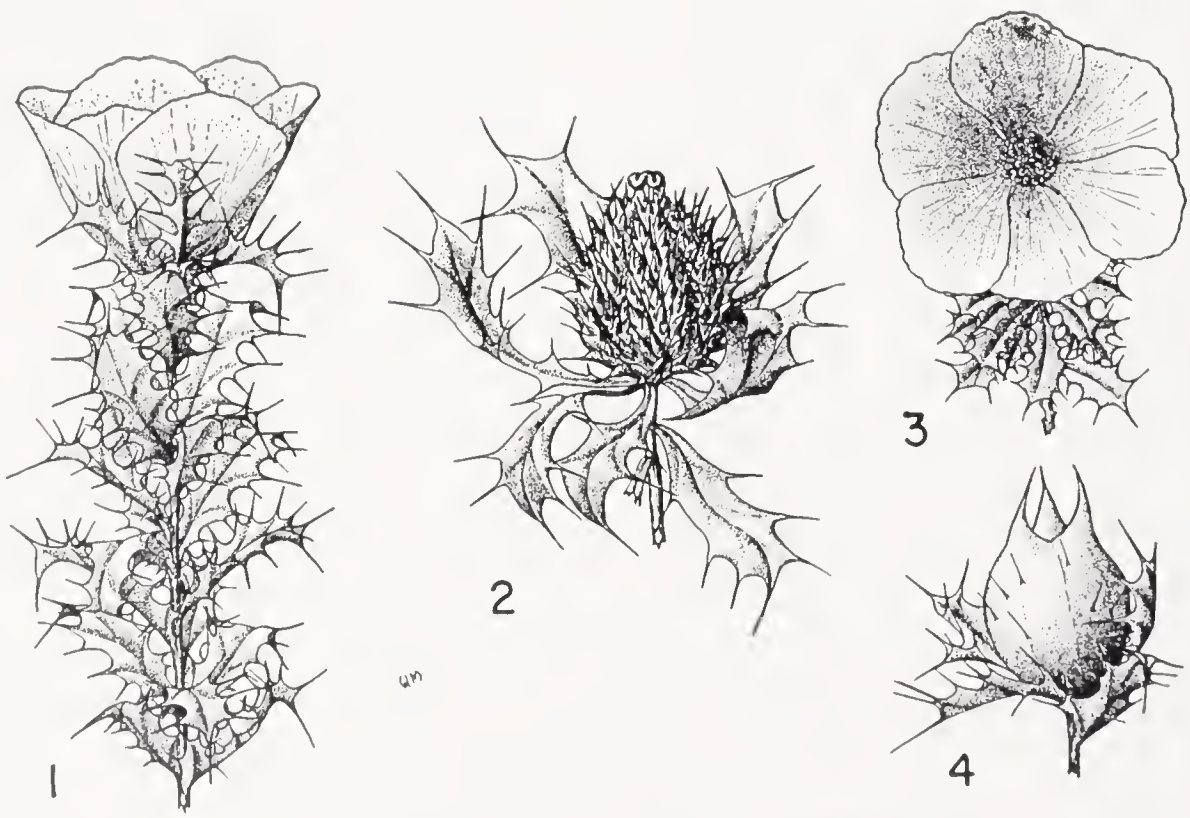

FIG. 1. *A. fruticosa*. 1. Flowering branch × ½. *Hinton et al.* 16582 (US). 2. Capsule × 1. *Palmer* 21 (GH). 3. Open flower × ½. Same as 2. 4. Bud × 1. Same as 2.

Habitat and distribution: Rocky slopes, hills and canyons, southern Coahuila in the mountains near Parras, at elevations of probably 5500 to 6000 ft.

Flowering and fruiting dates: Evidently flowers from May 1 onward through the summer; fruits mature a month or more after flowering.

A. fruticosa is not closely allied to any other species. It is distinctive in its shrubby habit, coriaceous leaves which Prain rightly described as holly-like, its persistent leaf bases, and its tuberculate-spinescent, broadly ovate capsules as well as in many other characters. Prain, l.c., describes the capsules as dehiscing nearly to the base, a character I have not been able to observe in the material before me. If true, this is another important distinguishing feature of the species as all of the others dehisce only in the upper portion. This is only a matter of degree, however, and this character, if verified, constitutes no more than an additional specific distinction. The morphological features setting *A. fruticosa* apart are not sufficient, in the writer's opinion, to justify removing the species from the genus.

This species is a local endemic and, although it has been known for over 100 years, adequate collections have never been distributed. New and ample collections made at various times of year would doubtless be of material value in gaining a more complete knowledge of the species. *A. fruticosa* and *A. subintegrifolia* are the only North American species of *Argemone* that the writer has not personally studied in the field.

Specimens examined: MEXICO.

COAHUILA

S. Lorenzo de Laguna, 7 miles s.w. from Parras, *Palmer* 21 (GH, US); San Lorenzo de Laguna and vicinity, 22 to 27 leagues s.w. from Parras, *Palmer* 1064 (US); Villareal, *Purpus* 4646 (F, MO, UC); S. Paila (Valle Yucatán), alt. 1700 m., *Hinton et al.* 16582 (GH, US); mountain pass, La Peña, *Thurber* 844 (GH, lectotype of *A. fruticosa* Thurber ex Gray; isotypes, MO, N.Y).

2. ARGEMONE MEXICANA L., Sp. Pl. 1: 508. 1753.

A. mexicana [Tournef., Élémens de Bot., p. 204, t. 121. 1694; Tournef., Inst. Rei Herb., 1: 239, 2: t. 121. 1700]; L., Syst. Nat., ed. 10, 2: 1073. 1759; Miller, Gard. Dict., ed. 7. 1759; Miller, Figures 1: 33, t. 50. 1759; Lamarck, Encycl. Méth. 1: 247. 1783; Gaertn., Fruct. et Sem. Pl. 1: 287; t. 60. 1788; Walter, Fl. Carol., p. 153. 1788; Aiton, Hort. Kew., ed. 1, 2: 225. 1789; Vitm., Summa Pl. 3: 297. 1789; Curtis, Bot. Mag. 7: t. 243. 1794; Lamarck, Planches 2: t. 452. 1797; Lestib., Bot. Belg. ed. 2, pt. 3, 2: 131. 1799; Willd., Sp. Pl. 2: 1148. 1799; Pers., Syn. Pl. 2: 62. 1807; Aiton, Hort. Kew., ed. 2, 3: 290. 1811; Luman, Hort. Jamaic. 2: 312. 1814; Pursh, Fl. Am. Sept. 2: 366. 1814, excluding white-flowered variety; Hornem., Hort. Hafn., p. 489. 1815; Nutt., Gen. 2: 9. 1818, excluding white-flowered species; DC., Reg. Veg. Syst. Nat. 2: 85. 1821; DC., Prodr. 1: 120. 1824; Elliott, Bot. Carol. & Georg. 2: 13. 1824, excluding white-flowered variety; Spreng., Syst. Veg., ed. 16, 2: 604. 1825, excluding *A. alba* Raf., in synonomy; Darlingt., Fl. Cest., p. 57. 1826; Loud., Hort. Brit., p. 216. 1830; Roxb., Fl. Ind. 2: 571. 1832; Beck, Botany, p. 21. 1833, in part; Hook., in

Journ. Bot. 1: 190. 1834, as to Drummond 15; Wight & Arn., Prodr. 1: 18. 1834; Blanco, Fl. de Filip., p. 454. 1837; Torrey & Gray, Fl. N. Am. 1: 61. 1838, excluding varieties β, γ, and white-flowered forms in references cited; Wight, Ill. Ind. Bot. 1: t. 11. 1840; Walp., Rep. 1: 109. 1842, excluding varieties; Gray, Man., ed. 1, p. 26. 1848, excluding white-flowered component; Gray, Gen. 1: 111, t. 47. 1849; Walp., Ann. 2: 26. 1852, in part; Seemann, Bot. Voy. H.M.S. Herald, pp. 23, in part, 78, 363. 1852-1857; Darlingt., Fl. Cest., ed. 3, p. 13. 1853; Hook. f. & Thoms., Fl. Ind. 1: 251. 1855; Mueller, in Walp., Ann. 4: 170. 1857, in large part; Chapm., Fl. So. U. S., p. 21. 1860, excluding white-flowered plants; Griseb., Fl. Br. W. Ind., p. 13. 1864; Oliv., Fl. Trop. Afr. 1: 54. 1868; Hook. f. & Thoms., in Hook., Fl. Br. Ind. 1: 117. 1872; Baker, Fl. Maurit., p. 5. 1877; Blanco, Fl. Filip., Gran. ed., 2: 220. 1878; Hemsl., Biol. Cent. Am., Bot. 1: 27. 1879, in part; Fern.-Vill., Nov. App., in Blanco, Fl. Philip., 4(3): 9. 1880; Hemsl., Biol. Cent. Am., Bot. 4: 97. 1887; Hemsl., l.c., p. 111; Balf., Bot. Socotra, in Trans. Royal Soc. Edinb. 31: 3. 1888; Prantl & Kündig, in Engl. & Prantl, Nat. Pflanzenf. 3 (2): 135, 141. 1889, excluding fig. 83B; Coulter, in Contr. U. S. Nat. Herb. 2: 12. 1891; Kuntze, Rev. Gen. 1: 12. 1891; Gray, Syn. Fl. N. Am. 1 (1): 87. 1895; Britton & Brown, Ill. Fl. 2: 101. 1897; Chapm., Fl. So. U. S., ed. 3, p. 20. 1897, as to yellow-flowered plants; Urbina, Cat. Pl. Mex., p. 5. 1897, as to name only, not as to cited specimens; Smith, in Pittier, Primit. Fl. Costar. 2: 18. 1898; Mohr, Pl. Alab., in Contr. U. S. Nat. Herb. 6: 520. 1901; Britton, Man., p. 439. 1901; Rose, in Contr. U. S. Nat. Herb. 8: 24. 1903; Small, Fl. s.e. U. S., p. 462. 1903; Urban, Sym. Ant. 4:250. 1905; Rydb., Fl. Colo., p. 149. 1906; Robins. & Fern., in Gray's Man., ed. 7, p. 416. 1908, excluding var. *ochroleuca*; Fedde, in Pflanzenr. 4 (104): 273, 274, fig. 36B. 1909, excluding *Pringle* 8321; Boldingh, Fl. Ned. W. I., p. 194. 1913; Britton & Brown, Ill. Fl., ed. 2, 2: 139. 1913; Small, Fl. Flor. Keys, p. 52. 1913; Fawc. & Rendl., Fl. Jamaica 3: 221. 1914; Rydb., Fl. R. Mts., p. 317. 1917; Britton, Fl. Berm., p. 144. 1918; Urban, Sym. Ant. 8: 236. 1920; Britton & Millsp., Bahama Fl., p. 145. 1920; Rydb., Fl. Pr. & Pl., p. 353. 1932; Small, Man. S. E. Fl., p. 548. 1933; Stahl, Fl. Puerto Rico, ed. 2, 1: 80. 1936; Stehlé et al., Fl. Guad. 2 (1): 32. 1937; Stemen & Myers, Okla. Fl., p. 162. 1937; Gates, Fl. Kans., p. 156. 1940; Moscoso, Cat. Fl. Dom., p. 204. 1943; Standl. & Steyerm., Fl. Guat., Fieldiana: Botany 24 (4): 348. 1946, in part; Stevens, Kans. Wild Fl., p. 116. 1948; Fernald, Gray's Man., ed. 8, p. 681. 1950; Gleason, New Ill. Fl. 2: 199. 1952; Harringt., Man. Pl. Colo., p. 252. 1954; Jones & Fuller, Vasc. Pl. Ill., p. 221. 1955.

Papaver spinosum [Bauhin, Phytopinax, p. 311. 1596; Bauhin, Pinax, p. 171. 1623].

Carduus Chrysanthemus Peruanus [Gerard, Herbal, p. 993. 1597].

Ectrus trivialis Lour., Fl. Cochinch. 1: 344. 1790; Steudel, Nomencl. Bot., ed. 2, 1: 543. 1840 (misspelled *trivalvis*).

Argemone spinosa Moench, Meth. Pl., p. 227. 1794; Sheent, Fl. Carol. 1: 202. 1806.

A. versicolor Salisb., Prod. Stirp., p. 376. 1796.

L'Argemone du Mexique Tourn., Élém. Bot., éd. aug., 2: 12, 5: t. 121. 1797.

Argemone serratis Stokes, Bot. Mat. Med. 3: 195. 1812.

A. vulgaris α Spach, Hist. Nat. Veg. 7: 26. 1839.

A. mucronata Dum. Cours. ex Stendel, Nomencl. Bot., ed. 2, 1: 128. 1840.

A. mexicana α *lutea* Kuntze, Rev. Gen. 1: 12. 1891.

A. mexicana α *lutea* var. *parviflora* Kuntze, l.c.

A. mexicana var. *typica* Prain, in Journ. Bot. 33: 308. 1895.

A. mexicana var. *ochroleuca* Britton, Man., p. 439. 1901; not *A. ochroleuca* Sweet.

Ectrus mexicanus Nieuwland, in Am. Midl. Nat. 3: 350. 1914.

Annual with bright yellow latex; stems mostly 1, 2.5-8.0 (-10.0) dm. tall, often branched from near the base, smooth (in f. *leiocarpa*) or rather sparingly prickly with perpendicular or slightly reflexed prickles; leaves glaucous, the light blue markings over the veins conspicuous, oblanceolate below, progressively broadly elliptical to ovate above, the middle and upper ones mostly very evidently clasping the stem, the lamina lobed to one-half or more of the distance to the midrib in the lower leaves, more shallowly lobed upward, the lobes oblong, the sinuses comparatively narrow, the acute mar-

ginal teeth tipped with a slender spine, both lower and upper surfaces of the leaves totally smooth (in f. *leiocarpa*) or the lower surfaces sparingly prickly on the main veins, the upper surfaces very distantly prickly on the main veins or totally smooth; buds subspherical or barely oblong, the body 9-13 mm. broad, 10-15 mm. long, totally smooth (in f. *leiocarpa*) or very sparingly prickly, the sepal horns terete, 5-10 mm. long including the apical spine, smooth; flowers 4-6 (-7) cm. in diameter, closely subtended by 1 or 2 foliar bracts; petals bright yellow or evidently sometimes pale yellow, the outer obovate, the inner obovate to obcuneate; stamens 30-50, the filaments pale lemon-yellow, the anthers yellow; stigma purple, about 1.5-4.0 mm. wide by 1.0-2.0 mm. high, the lobes pressed against each other and appressed to the style at anthesis, the non-receptive tissue between the lobes usually not visible in living state at this stage; style to about 1.0 (-3.0) mm. long in fruit; capsules 4-6-carpellate, oblong to broadly elliptical, the width, excluding the spines if present, 12-20 mm., the length, including the stigma and style, 25-45 mm., the surface totally smooth (in f. *leiocarpa*) or spinescent, then the armature consisting mostly of large, rather even-sized spines, the longest of which is about 6-10 mm., a very few lesser spines or prickles sometimes present, the capsular surface clearly visible through the armature; seeds 1.6-2.0 mm. long. (Ill.: Fig. 2, 1-3; Dist.: Fig. 5.)

Holotype: The specimen of *Argemone* in the Linnaean Herbarium marked by Linnaeus himself as *Argemone mexicana* (not seen; photographs, F, GH, US). See B. D. Jackson (1907, 1912) and Savage (1945).

Habitat and distribution: Waste places, often a weed along roadways and in dooryards and fields; doubtless native to the West Indies and probably also native in parts of Central America and Florida, but probably entirely introduced in Mexico except on the Yucatan Peninsula; now cosmopolitan in distribution through introduction into all tropical and subtropical parts of the world. In eastern United States the species is frequently introduced and is persistent for indefinite periods; probably it is not fully naturalized except in Florida and in coastal areas of the southern and southeastern states. In the distributional range herein considered, *A. mexicana* occurs at elevations of near sea level, generally, to 5000 ft. or more in Central America.

Flowering and fruiting dates: Flowers and fruits as local conditions permit at any time of the year.

Argemone mexicana was first described by Bauhin (1596) under the name *Papaver spinosum*. A year later Gerard (1597) described the same species under the name *Carduus chrysanthemus peruanus*. Tournefort (1694) first named the species *Argemone mexicana*. For taxonomic purposes, the use of the name derives from its acceptance by Linnaeus (1753).

Several post-Linnaean authors have proposed new names for *A. mexicana*. *A. spinosa* Moench represents an attempt to revive the oldest specific epithet for this species. *A. versicolor* Salisb. was a substitute name, evidently proposed because the author thought the current name inappropriate. *A. sexvalvis* Stokes was proposed to include those plants of *A. mexicana* with six valves or placentae in each capsule, a wholly superficial criterion since the number of valves is variable even on a single plant. *A.*

FIG. 2. 1-3. *A. mexicana*. 1. Bud × 1. From living plants, cult., Univ. of Minn. 2. Capsule × 1. Same as 1. 3. Habit × 1. Same as 1. 4. *A. mexicana* f. *leiocarpa*. Capsule × 1. *Curtis* 5653, *in part* (MIN).

vulgaris Spach is a composite species including three elements. The first element, his var. α is equivalent to *A. mexicana* L. *A. mucronata* Dumont de Courset is merely a listing of the name by Steudel and one has only Steudel's word that it is referable to *A. mexicana*. Kuntze's *A. mexicana* α *lutea* probably is intended to include all of the yellow-flowered argemones. Certainly his var. *parviflora* of α *lutea* is not separable from typical *A. mexicana*. *Ectrus trivialis* was proposed through lack of knowledge of the nomenclatorial history of the species.

The identity of *A. mexicana* is fully established by means of the holotype in the Linnaean Herbarium. I have seen a photograph of the holotype taken by the Linnaean Society in 1942. The plant shown is undoubtedly of Antillean stock.

The species is readily distinguished by its usually bright yellow petals, low stamen number and typically clasping, comparatively shallowly lobed middle and upper cauline leaves. It is most often confused with *A. ochroleuca* subsp. *ochroleuca*. The ways by which these two taxa can be distinguished are discussed under the latter species. *A. ochroleuca* Sweet has often been treated as a variety of *A. mexicana*. In my opinion the two should not be united.

Plants of *A. mexicana* with pale yellow flowers (sometimes said to be white; see Standley & Steyermark, 1946) have been collected in Costa Rica, El Salvador, Nicaragua, and Guatemala. The overall aspect of many of these plants also differs from that typical of the species as it occurs in the West Indies. The difference, if real, may be defined as a tendency toward narrower, more deeply lobed leaves, the marginal teeth more acute and with longer terminal spines. I place these aberrant Central American specimens in *A. mexicana* proper with reservations.

A. mexicana is one of those remarkable weeds which has spread throughout the world in tropical and subtropical regions in post-Columbian times. It is a common weed around seaport towns and it has been supposed that this has promoted the incidental transport of seeds along the seaways to similar localities in other parts of the world from which it has subsequently spread. Another feature of *A. mexicana* previously unreported is the high degree of self-compatibility of the individual plants. This means that a single viable seed may lead to the establishment of the species in a new locality. The seeds themselves retain their viability for at least several, perhaps many years.

Specimens examined: UNITED STATES.

ALABAMA

Mobile Co.: banks, Mobile river, *Mohr s.n.* (US).

CONNECTICUT

New Haven Co.: New Haven, *Kleeberger s.n.* (CAS).

FLORIDA

Collier Co.: Marco, *Standley* 12737 (US). Columbia Co.: Lake City, *Rolfs* 1075 (F). Dade Co.: Brickell Hammock, Miami, *Moldenke* 523 (MO, NY, US); Addison Hammock, *Small* 7481 (GH, NY, US). Duval Co.: Jacksonville, *Churchill s.n.* (GH, MO). Escambia Co.: Pensacola, *Tracy s.n.* (MO, NY). Franklin Co.: Apalachicola, *Chapman s.n.* (NY). Hillsborough Co.: Tampa, *Barnhart* 2234 (F, NY). Jefferson Co.: Monticello, *Lighthipe s.n.* (F). Lee Co.: Fort Myers, *Standley* 13033 (US). Monroe Co.: Key West, *Curtiss* 5653, *in part* (F, GH, KSC, MIN, MO, NY, POM, UC, US); Key West, *Pollard, Collins & Morris* 1 (F, MIN, ND, NY, US); Key West, *Rugel* 15 (NY). Polk Co.: Lakeland, *McFarlin* 4407 (CAS). St. Johns Co.: moat of Ft. San Marco, St. Augustine, *Smith s.n.* (US). Volusia Co.: New Smyrna, *Burgess* 574 (F. NY).

GEORGIA

Glynn Co.: Brunswick, *Small s.n.* (F, NY). McIntosh Co.: Darien, *Smith* 2123 (F).

ILLINOIS

Menard Co.: Athens, *Hall s.n.* (F). Stephenson Co.: Freeport, *Johnson s.n.* (NY, US).

KANSAS

Douglas Co.: no locality, *Snow* 114 (KANU).

LOUISIANA

Orleans Parish: New Orleans, *Drummond* 15 (GH). Plaquemines Parish: the Mississippi delta and adjacent islands, Port Eads, *Lloyd & Tracy* 294 (NY).

MARYLAND

Prince Georges Co.: Bladensburg, *Leonard* 17568 (US).

MASSACHUSETTS

Hampshire Co.: South Hadley, *Cook s.n.* (US). Middlesex Co.: Cambridge, *Morong s.n.* (NY).

MISSISSIPPI

Adams Co.: Natchez, *Shimek s.n.* (F).

MISSOURI

Franklin Co.: Pacific, *Kellogg* 1754 (MO). St. Louis, City, *Ketlog s.n.* (US). Wayne Co.: Piedmont, *Trelease s.n.* (MO).

NEBRASKA

Sarpy Co.: Bellevue, *Hayden s.n.* (MO).

NEW JERSEY

Cape May Co.: Cape May, *MacKenzie* 6680 (NY). Hunterdon Co.: Annandale, *Fisher s.n.* (NY).

NEW YORK

Westchester Co.: Tarrytown, *Barnhart* 661 (NY).

PENNSYLVANIA

Philadelphia Co.: Philadelphia, *Parker s.n.* (F, GH).

South Carolina

Beaufort Co.: Beaufort, *Churchill s.n.* (GH, MIN, MO). Charleston Co.: Charleston, *Stewart s.n.* (F).

Tennessee

Davidson Co.: Nashville, *Gattinger s.n.* (US).

Texas

Bexar Co.: San Antonio, *Jermy s.n.* (NY). Cameron Co.: Brownsville, *Runyon s.n.* (TEX). Hildalgo Co.: 8 miles s. of Alamo, *Clover* 778 (CAS, DS). Real Co.: Leakey, *Cory* 44481 (TEX). Travis Co.: Austin, *Tharp* s.n. (TEX). Webb Co.: Laredo, *Reverchon s.n.* (MO).

Virginia

Frederick Co.: Winchester, *Hall s.n.* (F).

Washington, D. C.

Washington, *Steele s.n.* (US).

BAHAMA ISLANDS.

Acklin's I.: Spring Point, *Brace* 4512 (F). Eleuthera I.: no locality, *Hitchcock s.n.* (MO). Fortune I.: no locality, *Hitchcock s.n.* (MO). Grand Turk I.: no locality, *Millspaugh & Millspaugh* 8988 (F, NY). Great Bahama I.: Eight Mile Rocks, *Britton & Millspaugh* 2366 (F, NY). Great Inagua I.: Matthew Town, *Nash & Taylor* 1356 (NY). New Providence I: Nassau, *Wight* 7 (F, GH, NY). North Bimini I.: no locality, *Howard & Howard* 10099 (SMU, US).

BERMUDA.

Spanish Point, *Brown & Britton* 182 (F, GH, NY, US); near Fraseati, *Collins* 192 (F, GH, NY, US); The Flatts, *Moore* 2854 (CAS, GH).

WEST INDIES. Cuba

Santiago de las Vegas, *Baker & Wilson* 529 (CAS, F, MIN, POM, UC, US); Rodas, *Combs* 485 (F, GH, MO, NY); Pinar del Río, *Palmer & Riley* 387 (NY, US); Colonia Limones, Ingenio Soledad, near Cienfugos, *Pringle* 50 (GH, US); Santiago, *Underwood & Earle* 170 (NY); Herradura, *Van Hermann* 578 (F, NY).

Dominican Republic

Guayubín, alt. 100 m. or less, *Abbott* 909 (US); Piedra Blanca, alt. 200-500 m., *Allard* 14477 (US); Santiago, Eggers 1995 (US); San Cristóbel, *Faris* 62 (US); Habanera, am Yaqui Fluss, Prov. Barahona, alt. 50 m., *Fuertes* 138 (F, GH, MIN, MO, NY, US); Hondo Valle, alt. 3500 ft., *Howard & Howard* 8784 (NY); Azua, *Rose, Fitch & Russell* 3899 (NY, US); Monción, alt. 375 m., *Valeur* 149 (F, MO, NY, US).

Haiti

Emnery, alt. 330 m., *Ekman* H. 9667 (US); Port au Prince, *Leonard* 2809 (NY, US); St. Mare, *Leonard* 2899 (GH, US); Fond Parisien, Etang Saumatre, *Leonard* 4170 (GH, US); Gros Morne, alt. 235 m., *Leonard* 9895 (GH, NY, US); Tortue I., *Leonard & Leonard* 15605 (US).

Jamaica

Mandeville, *Churchill s.n.* (GH); Kingston, alt. 500 ft., *Clute* 25 (MIN, MO, US); Grand Cayman I., Georgetown, *Millspaugh* 1400 (F).

Leeward Islands

Antigua I.: no locality, *Rose, Fitch & Russell* 3416 (US). Dominica I.: West Cabrit, Portsmouth, alt. 183 m., *Hodge* 3707 (GH). Guadeloupe Is.: Basse Terre, Les Saintes, Marie Galante Islands, *Duss* 2434 (F, GH, MO, NY, US); Capesterre, alt. 25 m., *Stehlé* 630 (US). St. Kitts I.: Basseterre, *Britton* 759 (NY).

Puerto Rico

San Juan, *Heller & Heller* 313 (F, NY); 7 miles s. of Caguas, alt. ca. 2300 ft., *Heller & Heller* 313 (US); Guánica, *Millspaugh* 709 (F); Ponce, *Prey* 3 (US); Vieques I., Isabel Segunda to Mosquito, *Shafer* 2845 (NY, US); no locality, *Wydler s.n.* (NY).

Virgin Islands

St. Croix I.: Bassin field, *Ricksecker* 101 (F, GH, MIN, MO, NY, UC, US). St. Thomas I.: no locality, *Eggers s.n.* (MIN, MO); no locality, *Eggers* 204 (GH, UC). Tortola I: Exp. Sta., *Fishlock* 10 (NY, US). Virgin Gorda I.: no locality, *Fishlock* 196 (NY).

Windward Islands

Barbados I.: St. Michael, *Barrow* 8 (NY, US). Bequia I: no locality, *Joseph* B.233 (NY). Grenada I.: Grand Anse, *Broadway s.n.* (F, GH, NY). Martinique I.: Ste. Anne, *Duss* 1776 (NY).

MEXICO. Campeche

Campeche, *Goldman* 527 (US); Tuxpeña, *Lundell* 1122 (DS, F, MO, NY, US); Champotón, *Steere* 1719 (F).

Guerrero

Pungarabato, *Hinton et al.* 7283 (GH, NY, US); Acapulco, *Palmer* 553 (GH, US).

Nuevo León

Monterrey, alt. 500 m., *Abbon s.n.* (F, GH, UC); Sabinas Hidalgo, alt. 2000 ft., *Leavenworth* 53 (F); Montemorelos, *Nelson* 6698 (US).

Oaxaca

Between Llano Grande and Pinotepa, alt. 200-500 ft., *Nelson* 2337 (US); Oaxaca, *Rose & Hough* 4653 (US); near Tomellín, *Rose, Painter & Rose* 10090 (US); Cuicatlán, alt. 1800 ft., *Smith* 506 (GH).

Quintana Roo

San Miguel, Cozumel I., *Millspaugh* 1497 (F).

San Luis Potosí

19.3 miles s.w. of Nuevo Morelos (0.4 mile s.w. of Las Abritas), *Ownbey & Ownbey* 2045 (GH, MIN, US).

Tabasco

Entre la hacienda "El Cometa" y S. Juan Bautista, *Rovirosa* 98 (US).

Tamaulipas

Tampico, *Berlandier* 2 (F); Hacienda Santa Engracia, 40 miles n.w. of C. Victoria, alt. 240 m., *Meyer & Rogers* 2836, *in part* (MIN); 1.1 miles n. of El Limón (7.9 miles n. of El Mante), *Ownbey & Ownbey* 1414 (MIN); 24.2 miles s. of El Mante (38 miles n. of Valles), *Ownbey & Ownbey* 1418 (MIN); Tampico, alt. ca. 15 m., *Palmer* 111 (CAS, F, GH, K, MO, NY, US).

VERA CRUZ

Wartenberg, near Tantoyuca, *Ervendberg* 292 (NY); Veracruz, *Müller* 1855 (NY); Catemaco, alt. 1000 ft., *Nelson* 398 (US); Camarón, *Purpus* 8577 (GH, MO, NY, UC, US); Jalapa, alt. 4000 ft., *Smith* 1763 (NY).

YUCATÁN

South Kancabconot, *Gaumer* 23615 (F, GH, US); Izamal, *Gaumer* 562 (CAS, DS, F, GH, MO, NY, UC, US); Mérida, *Valdez* 16 (F, GH, MO, NY, US).

CENTRAL AMERICA. BRITISH HONDURAS

El Cayo, *Bartlett* 12965 (NY, US); America's Estate, Corozal Dist., *Gentle* 4958 (F, NY, US).

COSTA RICA

Alajuela, *Alfaro* 5705 (F, GH, US); Escasú, alt. ca. 1250 m., *Standley* 32375 (US); Cartago, *Stork* 300 (US).

EL SALVADOR

San Salvador, *Calderón* 189 (GH, NY, US); one-fourth mile s. of Santa Tecla, alt. ca. 625 m., *Carlson* 68 (CAS, F, MO, UC); Ahuachapán, alt. 800-1000 m., *Standley* 20232 (GH, US); San Vicente, alt. 350-500 m., *Standley* 21250 (US); Acajutla, alt. 30 m. or less, *Standley* 21939 (GH, US); Armenia, *Standley* 23464 (US).

GUATEMALA

La Libertad, *Aguilar* 399 (F); San Andrés, alt. 100-500 m., *Cook & Martin* 183 (US); Zacapa, alt. 620 ft., *Deam* 157 (GH); between Amatitlán and Palín, *Greenman & Greenman* 5877 (GH, MO); Santa Rosa, *Heyde & Lux* 2940 (GH, US); Casillas, *Heyde & Lux* 4307 (GH, US); Barranquilla, alt. 1800 ft., *Popenoe* 971 (US); Chilloin (?), alt. 1500 m., *Rójas* 68 (F, GH, MO, NY, US); Los Amates, alt. ca. 85 m., *Standley* 24353 (GH, US); Antigua, alt. 1500-1600 m., *Standley* 60381 (F); Jutiapa, alt. ca. 850 m., *Standley* 75821 (F); Chilapa, alt. ca. 895 m., *Standley* 78127 (F); Chimaltenango, alt. ca. 1830 m., *Standley* 80089 (F); Sayaxché, alt. 50 m., *Steyermark* 46281 (F, UC, US).

HONDURAS

n.e. of Zamorano, alt. 850 m., *Molina* 883 (F); Comayagua, alt. ca. 600 m., *Standley & Chacón* 6040 (F).

NICARAGUA

Managua, *Baker* 700 (POM, US); between Managua and Asososca, *Greenman & Greenman* 5646 (GH, MO); Sangsangta Dist., *Schramm s.n.* (F); Sierra de Managua, region of Los Nubes, *Standley* 8709 (F); Esteli, alt. ca. 680 m., *Standley* 20224 (F).

PANAMA

Santa Rita Trail, *Cowell* 114 (NY).

2a. ARGEMONE MEXICANA L. f. **leiocarpa** (Greene) G. B. Ownb., stat. nov.

A. leiocarpa Greene, in Pittonia 3: 345. 1898; Small, Fl. s.e. U. S., p. 462. 1903; Fedde, in Pflanzenr. 4 (104): 278, 274, fig. 36E. 1909; Small, Fl. Flor. Keys, p. 52. 1913; Small, Man. s.e. Fl., p. 548. 1933.

A. mexicana var. δ Torr. & Gray, Fl. N. Am. 1: 61. 1838.

A. mexicana var. *leiocarpa* Prain, in Journ. Bot. 33: 311. 1895, provisional name with no taxonomic standing.

A. alba var. *leiocarpa* Fedde, in Pflanzenr. 4 (104): 279. 1909, nomen nudum in synonomy; not *A. alba* Lestib.

A. leiocarpa var. *mexicanoides* Fedde, l.c.

A. leiocarpa var. *ochroleucoides* Fedde, l.c.

A. mexicana var. *anacanthoidea* Fedde, l.c., nomen nudum in synonomy.

A. mexicana var. *ochroleuca* subvar. *inermis* Fedde, l.c., nomen nudum in synonomy; not *A. ochroleuca* Sweet.

Differs from the typical component of the species only in the stems, leaf surfaces, buds and capsules which are totally devoid of spines or prickles of any sort. (Ill.: Fig. 2, 4; Dist.: Fig. 5.)

Lectotype: *Charles L. Pollard, G. N. Collins and E. L. Morris* 2, collected at Key West, Florida (Plants of Subtropical Florida), March 9, 1899 (ND; isotypes, F, MIN, NY, US).

Habitat and distribution: Now occurring as a weed in disturbed or waste areas, southern Florida, Florida Keys and Dry Tortugas at elevations of near sea level. According to Prain (1895, p. 311-312) also found in West Africa and Brazil.

Flowering and fruiting dates: At any time of the year as local conditions permit; most commonly flowering from January to March and fruiting from February onward.

The distinguishing features of f. *leiocarpa* are maintained even when it is growing with plants of typical aspect. Probably these differences are controlled by only one, or at most a very few genes. Until experimental evidence bearing upon its genetic relationship to *A. mexicana* proper is available for more exact determination of its status, its treatment as a forma seems fully justified.

Torrey and Gray, l.c., first noted that *A. mexicana* sometimes has smooth capsules. The distribution of their unnamed variety is given as Key West, and thus there can be no doubt that they referred to the present f. *leiocarpa*. They cite no collections or literature references. Prain, l.c., first suggested that the smooth capsuled *A. mexicana* be called var. *leiocarpa*. Greene followed Prain's suggestion by valid publication of the name but as a new species. Fedde attempted to separate Greene's *A. leiocarpa* into two components which he called varieties: var. *mexicanoides* included the lectotype of the species; var. *ochroleucoides* was a new segregate also based upon specimens from Key West. I have seen specimens of these two "varieties" which were annotated by Fedde (US). The differences pointed out by Fedde in capsule shape and style length are minor and are probably due more to a difference in age of the capsules than otherwise. There is no justification for separating f. *leiocarpa* into two components.

In his original discussion of *A. leiocarpa*, Greene mentioned collections made by Pollard and his companions from Key West. I have chosen to designate this the type collection of the forma although it was by no means the first time the plant was collected at this locality. Greene also mentions collections of the taxon sent to him from Tampa, Florida where they

were made by Tidestrom. I have turned up none of these latter specimens in any of the major herbaria in the United States and they may no longer be in existence.

It is of some interest to review the modern distribution of f. *leiocarpa*. It seems almost certain that this variant originated on the island of Key West where it occurs intermixed with plants of typical character. Its occurrence in south Florida and other islands could be entirely due to introductions. Similarly its occurrence in Brazil and West Africa is undoubtedly due to introductions of either the forma or of the typical phase of the species. One might speculate that if the differences between the typical phase of the species and the forma, genetically speaking, are really due to a single factor difference, then a single mutation resulting in the glabrous phase might occur more than once in widely separated parts of the species distribution.

Specimens examined: UNITED STATES.

FLORIDA

Dade Co.: outskirts of Florida City, *Ownbey & Ownbey* 1361 (MIN). Lee Co.: Myers, July, *Hitchcock s.n.* (F). Hillsborough Co.: no locality, *Fredholm* 6250 (GH, MO, US). Monroe Co.: Key West, *Curtiss* 5653, *in part* (US, holotype of *A. leiocarpa* var. *ochroleucoides* Fedde; isotypes, F, GH, KSC, MIN, MO, UC, US); Garden Key, Tortugas group, *Lansing* 2531 (F); Key West, *Pollard, Collins & Morris* 2 (ND, lectotype of *A. leiocarpa* Greene; isotypes, F, MIN, NY, US; also type collection of *A. leiocarpa* var. *mexicanoides* Fedde, holotype, US); Crawl Keys, *Small & Carter* 2962 (NY); near Flamingo, *Small* 7656 (NY, US); Loggerhead Key, Dry Tortugas, *Taylor s.n.* (NY). Polk Co.: Carter's Corner, vicinity of Lakeland, *McFarlin* 4469 (CAS).

3. ARGEMONE OCHROLEUCA Sweet, Brit. Fl. Gard. 3: t. 232. 1829.

Annual or short-lived perennial with bright yellow to orange latex; stems 1-few, 3-10 (-12) dm. tall, branched in the upper portion, armed with widely spaced, perpendicular or slightly reflexed stoutish prickles; leaves very glaucous, the light blue areas over the veins very conspicuous, the largest basal leaves sometimes 35 cm. or more long, oblanceolate, the middle and upper leaves elliptical to ovate, not clasping, or the uppermost ones slightly clasping, both basal and cauline leaves mostly deeply lobed to near the midrib, the lobes oblong, the lower surfaces distantly prickly on the veins, the upper surfaces weakly and very sparingly prickly on the veins or more often totally smooth; buds oblong, the body 4-11 mm. wide, 8-18 mm. long, with about 3-6 or more fine prickles on each sepal, the slender sepal horns round in cross-section, smooth, 5-12 mm. long including the slender terminal spine; flowers 3-7 cm. in diameter, closely subtended by 1-2 bracteate leaves; petals very pale lemon-yellow, lemon-yellow or rarely darker yellow, obcuneate, obcuneate-obovate or narrowly elliptical; stamens about 20-75, the filaments pale yellow, the anthers darker yellow; stigma purple, about 2-3 mm. wide and 1.0-1.5 mm. high, the lobes spreading, the bluish, non-receptive surfaces between them usually clearly visible; style evident in fruit, about 1-3 mm. long; capsules 3-6-carpellate, lanceolate, ovate-lanceolate to occasionally oblong-elliptic, the width, excluding the spines, 10-18 mm., the length, including the stigma and style, 20-50 mm., the armature consisting of stout, rather even-sized spines, these sometimes interspersed with smaller spines, the larger spines spreading or visibly reflexed, well-spaced, about 6-12 mm. long, the capsular surface clearly visible through the armature; seeds 1.5-2.0 mm. long.

Holotype: Sweet, l.c., states that "The specimens from which our drawing was made, were kindly sent to us by Robert Barclay, Esq. in whose superb collection at Bury-Hill they were raised last Spring from seeds received from Mexico, ..." At the Royal Botanic Gardens, Kew, there is preserved a specimen of *A. ochroleuca* cultivated in Barclay's garden. It probably is not possible at this date to establish that this specimen positively was the material from which the original description and illustration of the species were drawn. I think, however, that the probability of this being the case is sufficiently great that this specimen may be designated the holotype. The illustration accompanying the original description is of such excellence that the identity of the species is unmistakable.

Key to the subspecies:

1. Buds, excluding the sepal horns, 8-11 mm. wide x 15-18 mm. long; flowers 4-7 cm. in diameter; petals obcuneate, lemon-yellow; capsule armature of rather even-sized large spines with few if any smaller ones . . . . . 3a. *A. ochroleuca* subsp. *ochroleuca*
1. Buds, excluding the sepal horns, 4-6 mm. wide x 8-12 mm. long; flowers 3-5 cm. in diameter; petals narrowly elliptical, pale lemon-yellow; capsule armature of larger spines intermingled with smaller spines and prickles . . . . . 3b. *A. ochroleuca* subsp. *stenopetala*

3a. Argemone ochroleuca Sweep subsp. ochroleuca

A. ochroleuca Sweet, Brit. Fl. Gard. 3: t. 242. 1829; Walp., Rep. 1: 110. 1842; Hemsl., Biol. Cent. Am., Bot. 1: 27. 1879; Rose, in Contr. U. S. Nat. Herb. 8: 25. 1903.

A. barclayana Penny ex Loud., in Gard. Mag. 6: 115. 1830; Loud., Hort. Brit., first add. suppl., p. 581. 1832, excluding *A. intermedia* Sweet, in synonomy.

A. mexicana var. *ochroleuca* Lindl., in Edward's Bot. Reg. 16: t. 1343. 1830; Prain, in Journ. Bot. 33: 310. 1895, as to Mexico distribution; Fedde, in Pflanzenr. 4 (104): 277, 274, fig. 36C. 1909, excluding Yucatan specimen cited; not *A. mexicana* L.

A. sulphurea Sweet ex Loud., Hort. Brit., p. 216. 1830.

A. mexicana var. β Torr. & Gray, Fl. N. Am. 1: 61. 1838; Walp., Rep. 1: 109. 1842; not *A. mexicana* L.

A. vulgaris β Spach, Hist. Nat. Vég. 7: 26. 1839.

A. mexicana Hemsl., Biol. Cent. Am., Bot. 1: 27. 1879, in part; Vasey & Rose, in Contr. U. S. Nat. Herb. 1: 65. 1890; Johnston, in Proc. Calif. Acad. 12: 1024. 1924; Gentry, Río Mayo Pl., in Carn. Inst. Wash. Pub. 527. 1942; Kearn. & Peeb., Fl. Pl. Ariz., p. 336. 1942; Kearn. & Peeb., Ariz. Fl., p. 324. 1951; not *A. mexicana* L.

A. platyceras Wats., in Proc. Am. Acad. 17: 318. 1882, as to *Parry & Palmer* 10; Hemsl., Biol. Cent. Am., Bot. 4:4. 1886, as to *Parry & Palmer* 10; not *A. platyceras* L. & O.

A. mexicana var. (*?*) Wats., in Proc. Am. Acad. 24: 38. 1888; not *A. mexicana* L.

A. mexicana var. *ochroleuca* "spp. *parviflora*" Prain, in Journ. Bot. 33: 310. 1895, nomen nudum; Fedde, in Pflanzenr. 4 (104): 277. 1909, nomen nudum; not *A. mexicana* L.

A. ochroleuca var. *barclayana* Prain, in Journ. Bot. 33: 325. 1895, provisional name having no taxonomic standing.

Annual or short-lived perennial; buds oblong, the body 8-11 mm. wide, 15-18 mm. long, the slender sepal horns 8-12 mm. long including the slender terminal spine; flowers 4-7 cm. in diameter; petals lemon-yellow, rarely darker yellow, the outer ones obcuneate, the inner ones obcuneate-obovate; stamens about 40-75; style in fruit 1-3 mm. long, rarely longer; capsules 4-5 (3-6) -carpellate, the width, excluding the spines, 14-18 mm.,

the length, including the stigma, 35-50 mm., the armature consisting of stout, rather even-sized spines, the larger spines 8-12 mm. long; longest dimension of seeds 1.5-1.8 mm. (Ill.: Fig. 3, 4-5; Dist.: Fig. 5.)

Holotype: That of the species.

Habitat and distribution: A common weed in disturbed soil along roadways, fields, arroyos, embankments, hills and intermountain plains throughout Mexico, except in the eastern lowlands and southern states, but most typical of the plateau region; also in the arid areas of western Mexico, Baja Canifornia del Sur and the Tres Marías Islands, its native area now indeterminable because of widespread introductions; reported from Australia. It occurs at sea level in western Mexico to altitudes of 7,500 feet on the central plateau of Mexico.

Flowering and fruiting dates: May be expected to flower and fruit during any month of the year where local conditions are suitable. Growth is most evident during the winter and early spring months in the dry areas of western Mexico; in the highlands of central Mexico the seasons of maximum flowering and fruiting are summer and fall.

A. ochroleuca subsp. *ochroleuca* is unknown to occur outside of Mexico except for introductions in Australia. I have seen one Australian specimen, *Smith* 363, from Kangaroo Pt. (GH). Doubtless there are other collections in Australian and English herbaria.

Both Prain and Fedde in their monographs of *Argemone* included much material from Argentina, Chile, Bolivia, Peru, Paraguay, Uruguay and Ecuador under *A. ochroleuca*. Most if not all of the specimens cited by these authors belong, not with *A. ochroleuca,* but with a native South American species, closely related to, but specifically distinct from *A. ochroleuca* and *A. mexicana.*

A. ochroleuca subsp. *ochroleuca* is most often confused with *A. mexicana.* Some principal differences between the two taxa were well stated by Sweet in the original description of *A. ochroleuca.* Sweet pointed out that *A. ochroleuca* had narrower, more deeply divided and sharper pointed leaves and distinctly spreading stigmas, *A. mexicana* having the stigmas closely crowded together. The stigmatic character is particularly useful. In *A. ochroleuca* the stigmatic lobes are divergent and not appressed to the style and the bluish non-receptive areas between them are visible. In *A. mexicana* the stigmatic lobes are appressed to the style and the non-receptive areas between them are ordinarily completely hidden by the receptive surfaces. *A. ochroleuca* also has pale lemon-yellow petals whereas *A. mexicana* has bright yellow petals but some intergradation in this feature is found. Another good difference resides in the buds, oblong in *A. ochroleuca,* more nearly subspherical in *A. mexicana.* In separating typical *A. mexicana* from var. *ochroleuca,* Prain referred to a difference in length of

style, "subnullo" in var. *typica,* "distincto" in var. *ochroleuca.* Most plants of *A. ochroleuca* do have a distinct style in fruit but the style in *A. mexicana* is also sometimes very evident. This distinction, therefore, seems to be of limited value.

Almost from the beginning there has been doubt among taxonomists as to whether *A. ochroleuca* should be accorded full specific rank or should be reduced to varietal status under *A. mexicana.* Soon after its original publication as a species by Sweet it was published as variety γ of a broadly drawn *A. mexicana* which also included *A. albiflora* by Lindley in the Botanical Register. Prain, (l.c., p. 325) with serious reservations followed Lindley. Fedde, (l.c., p. 277) also accorded *A. ochroleuca* only varietal rank; Rose, (l.c., p. 25) accorded *A. ochroleuca* full specific rank. In comparing it with *A. mexicana,* Rose pointed out the "somewhat thicker leaves, with stouter, more spinescent teeth" and said that in *A. ochroleuca* "The color of the flowers is pale lemon, while that of *mexicana* is always orange yellow."

In my opinion *A. mexicana* and *A. ochroleuca* are specifically distinct. Most of the confusion between the two arises from the study of pressed specimens; much immature material with inadequate data has accumulated in herbaria. In addition to the reasons already given for this treatment, there is also the distinctive distributional patterns of the two. Certainly these patterns are associated with distinctive environmental requirements. In several garden cultures that I have grown of both *A. ochroleuca* subsp. *ochroleuca* and *A. mexicana* the somatic number of chromosomes has always been 56 in the former and 28 in the latter. The two taxa are very much alike in cultural characteristics; both are easily grown in a single season from seeds; individual plants of either species are highly self-compatible.

A. Barclayana Penny (MSS., not seen) was a horticultural name taken up by Loudon, and was never adequately described. None of Penny's material is preserved at either Kew or the British Museum according to Prain (l.c., p. 325). Prain writes that a plant known as *A. Barclayana* was grown in English gardens for some years after the date of publication of the name. One of these garden specimens is preserved at Kew, and on this basis Prain associates the name *A. Barclayana* with the element of *A. ochroleuca* occurring in Baja California and coastal northwestern Mexico. There may, indeed, be a race of *A. ochroleuca* occupying the area specified by Prain as well as the Tres Marías Islands. I have not found sufficient basis for its taxonomic recognition to date. Whether this coastal element of *A. ochroleuca* is really identifiable with *A. Barclayana* Penny as averred by Prain has not been finally proved. For the present, *A. Barclayana* should remain a synonym of *A. ochroleuca* subsp. *ochroleuca.*

FIG. 3. 1-3. *A. ochroleuca* subsp. *stenopetala*. 1. Open flower × 1. Isotype, *Pringle* 43 (F). 2. Capsule × 1. Same as 1. 3. Habit × 1. Isotype, *Pringle* 43 (US). 4-5. *A. ochroleuca* subsp. *ochroleuca*. 4. Habit × 1. *Pringle* 8347 (US). 5. Capsule × 1. *Pringle* 11918 (US).

Two color forms of *A. ochroleuca* subsp. *ochroleuca* grow intermixed at Guaymas, Sonora. One form has the lemon-yellow petals of typical subsp. *ochroleuca*. The other form has bright yellow petals similar to those of *A. mexicana*. The two forms are not otherwise distinguishable. Although *A. gracilenta* sometimes occurs at the same localities, I am convinced that it is reproductively isolated under natural conditions and plays no part in the color variation in *A. ochroleuca*. The need for further study of subsp. *ochroleuca* from Guaymas is indicated.

I have observed several putative natural hybrids of *A. ochroleuca* subsp. *ochroleuca* X *A. pleiacantha* subsp. *pleiacantha* in the field. For a fuller discussion of this subject see the discussion under the latter taxon. A cytogenetic study of the two taxa and their hybrids is much needed.

Specimens examined: MEXICO.

AGUASCALIENTES

14.8 miles n. of Aguascalientes, Hwy. 45, *Ownbey & Ownbey* 1437 (MIN); 5 miles e. of Aguascalientes on road to San Luis Potosí, *Ownbey & Ownbey* 2038 (BM, GH, MEXU, MIN, NY, UC, US).

BAJA CALIFORNIA

Todos Santo, *Brandegee s.n.* (UC); La Paz, *Brandegee s.n.* (UC); San José del Cabo, *Brandegee s.n.* (UC); 26.5 km. s.e. of La Paz on road to Las Planes, *Carter* 2632 (DS, UC, US); Cape San Lucas, *Rose* 16946 (US); La Paz, *Palmer* 55 (GH, US); Cape San Lucas, *Xantus* 1 (US).

CHIHUAHUA

Presa de Chihuahua, *Le Sueur* 638 (CAS, F, MO, SMU, TEX, UC, US); 3.5 miles s.e. of Meoqui, *Ownbey & Ownbey* 1460 (ARIZ, BM, MICH, MIN, NY, UC); 31.0 miles n.e. of Hildalgo del Parral on road to Jiménez, *Ownbey & Ownbey* 1847 (MIN); 2.4 miles s.e. of Hidalgo del Parral, *Ownbey & Ownbey* 1849 (MICH, MIN); 14.4 miles s.w. of Chihuahua on road to Ciudad Guerrero, *Ownbey & Ownbey* 2011 (COLO, F, ILL, K, MIN); vicinity of Chihuahua, alt. about 1300 m., *Palmer* 152 (F, GH, MO, NY, US); valley near Chihuahua, *Pringle* 257 (F, GH, ND, NY, RSA, US); Chihuahua city, *Rose & Hough* 4207 (US); 6 miles w. of Camargo, alt. 4000 ft., *Shreve* 8069 (F); Sta. Eulalia, *Wilkinson* 4600 (NY); San Lorenzo, *Wislizenus* 282 (MO).

COAHUILA

Múzquiz, *Marsh* 21 (TEX); Monclova, *Marsh* 1675 (F, TEX); 23 miles s.w. of San Pedro, Hwy. 230, *Ownbey & Ownbey* 1450 (MIN, POM, SMU); Torreón, *Palmer* 477 (F, GH, MO, NY, UC, US).

COLIMA

Colima, *Palmer* 80 (US).

DURANGO

Durango, alt. 6300 ft., *Fisher* 44290 (MO, NY); 37.8 miles s.e. of turnoff to Villa Ocampo, Hwy. 45, *Ownbey & Ownbey* 1456 (GH, MEXU, MIN); 41.5 miles s.e. of Hidalgo del Parral, *Ownbey & Ownbey* 1856 (MIN); 17.3 miles s.w. of Ciudad Lerdo on road to Durango, *Ownbey & Ownbey* 1863 (MICH, MIN); 5.4 miles s.w. of Cuencamé on road to Durango, *Ownbey & Ownbey* 1867 (MIN); Durango, *Palmer* 241 (F, GH, MO, NY, UC, US).

FEDERAL DISTRICT

Mexico City, alt. 7300 ft., *Pringle* 8347 (F, GH, MEXU, MIN, MO, ND, NY, POM, RM, UC, US); about Mixcoac, alt. 7300 ft., *Pringle* 11918 (F, GH, US); near Guadalupe, *Rose & Hough* 4542 (US).

GUANAJUATO

Puerto de Nieto, *Kenoyer* 2036 (GH); 12.5 miles e. of Celaya, between Querétaro and León, *Ownbey & Ownbey* 2050 (CAS, F, GH, MIN, NY, UC); 5.1 miles n.w. of León on road to Lagos de Moreno, *Ownbey & Ownbey* 2051 (BM, MIN, MO, US).

GUERRERO

Placeres, *Hinton et al.* 9999 (NY, UC, US); Placeres-Cigarrillo, alt. 400 m., *Hinton et al.* 10014 (NY, TEX, US); Vallecitos, *Hinton et al.* 11789 (GH, NY, US).

HIDALGO

7.9 miles n. of Tasquillo, Hwy. 1, *Ownbey & Ownbey* 1421 (BM, F, MEXU, MICH, MIN, NY, UC, US); 14.1 miles s.e. of Ixmiquilpan, Hwy. 1, *Ownbey & Ownbey* 1422 (GH, MIN); 9.6 miles w. of junction of Hwy. 85 (to Mexico City) and Hwy. 45 (to Querétaro), *Ownbey & Ownbey* 2049 (MIN).

JALISCO

Puerta Vallarta, *Howell* 10325 (CAS); Guadalajara, *Jones s.n.* (CAS, DS, POM); between San Sebastián and Las Palmas, alt. 2000-3500 ft., *Nelson* 4133 (US); 37 miles s. of Guadalajara near w. end of Lake Chapala, *Ownbey & Ownbey* 1434a (GH, MEXU, MICH, MIN); n. of Lagos de Moreno, *Ownbey & Ownbey* 1436 (MIN); 11.6 miles n.e. of Tepatitlán, Hwy. 34, *Ownbey & Ownbey* 1435 (F, MIN); Guadalajara, *Woodruff s.n.* (NY).

MÉXICO

Near México, *Bourgeau* 6 (GH, US); Ypericones, alt. 1500 m., *Hinton* 3827 (GH, NY, US); Nanchititla, *Hinton et al.* 7355 (CAS, GH, K, NY, US); Naranjo, *Hinton et al.* 7520 (GH, K, NY); Amecameca, alt. 8600 ft., *Kuntze* 23651, *in part* (NY).

MICHOACÁN

Morelia, *Arsène* 3310 (NY, US); 2 km. w. of Zamora, alt. 1567 m., *Cutler* 4047 (F); Coalcomán, alt. 1000 m., *Hinton et al.* 12963 (GH, NY, US); 2.2 miles n.w. of Tuxpan, *Ownbey & Ownbey* 1430 (MEXU, MICH, MIN, US); 12.7 miles n.w. of Quiroga, *Ownbey & Ownbey* 1431 (MIN, UC); 1.0 mile e. of Carapán, *Ownbey & Ownbey* 1433 (MIN, NY); s.e. shore of Lake Pátzcuaro, alt. ca. 2200 m., *Schery* 149 (MO).

NAYARIT

Tepic, *Jones* 22844 (CAS, F, GH, NY, POM, UC); Acaponeta, *Jones* 23560 (CAS, GH, POM, UC); San Blas, *Maltby* 12 (US); Tres Marias Islands, *Mason* 1713 (CAS, K); same locality, *Mason* 1716 (CAS, F, NY); María Magdalena I., *Nelson* 4318 (US); vicinity of Acaponeta, *Rose, Standley & Russell* 14339 (NY, US).

PUEBLA

Rancho Posadas, vicinity of Puebla, alt. 2194 m., *Arsène & Nicolas* 62 (GH, MO, US); near Puebla, alt. 2150 m., *Grant* 560 (F, GH); San Baltazar, *Nicolas* 50 (F); Chalchicomula, *Smith s.n.* (MO).

QUERÉTARO

Querétaro, *Arsène* 10055 (US).

San Luis Potosí

2.7 miles n.e. of Villa de Hidalgo, *Ownbey & Ownbey* 2042 (GH, MIN, UC, US); region of San Luis Potosí, *Parry & Palmer* 10 (GH, MO, US).

Sinaloa

Imala, *Gentry* 5933 (DS, MO, NY); Culicán, *Goldman*, 368 (GH, NY, US); Villa Unión, *Lamb* 406 (DS, GH, MO, ND, NY, US); San Ignacio, alt. 260 m., *Ortega* 133 (CAS, US); Mazatlán, *Ortega* 6643 (CAS, MIN, US); vicinity of Fuente, *Rose, Standley & Russell* 13476 (NY, US); vicinity of Villa Unión, *Rose, Standley & Russell* 13889 (NY, US); vicinity of Mazatlán, *Rose, Standley & Russell* 14015, 14016 (NY, US); vicinity of Guadalupe, *Rose, Standley & Russell* 14758, 14769 (NY, US).

Sonora

San Bernardo, Río Mayo, *Gentry* 1337 (F, GH, MEXU, MO, UC); 13.2 miles e. of Moctezuma on road to Huasabas, *Ownbey & Ownbey* 1775 (ARIZ, CAS, GH, MEXU, MIN, NY, RSA, UC, US); 27.9 miles s.w. of Moctezuma, *Ownbey & Ownbey* 1777a (GH, MIN, US); 1.5 miles s. of El Oasis, Magdalena-Hermosillo road, *Ownbey & Ownbey* 2085 (MIN); 4.0 miles n. of Imuris, Magdalena-Nogales road, *Ownbey & Ownbey* 2093 (MIN); Guaymas, *Palmer* 105 (GH, ND, NY, US); vicinity of Hermosillo, *Rose, Standley & Russell* 12399 (NY, US); vicinity of Alamos, *Rose, Standley & Russell* 12913 (GH, NY, US); vicinity of Navojoa, *Rose, Standley & Russell* 13125 (NY, US); vicinity of Guaymas, *Rose, Standley & Russell* 15012 (NY, US); same locality, *Rose, Standley & Russell* 15013 (NY, US); Río Yaqui, Torín, alt. 100 ft., *Studhalter* 1458 (US); Río Moctezuma, Moctezuma, *White* 325 (GH).

Tamaulipas

Vicinity of Victoria, alt. about 320 m., *Palmer* 79 (F, GH, K, MO, NY, US); vicinity of Tampico, alt. about 15 m., *Palmer* 315 (CAS, F, GH, K, MO, NY, US).

Tlaxcala

Mt. Malinche, San Francisco (Tetlanochan), alt. 7500 ft., *Balls*, B4899 (UC).

Vera Cruz

Orizaba, *Nelson* 188 (US); Orizaba, *Smith* 127 (MO).

Zacatecas

Ojo Caliente, *Jones* 86 (MO, POM, US); 17.1 miles n.w. of Sombrerete, Hwy. 45, *Ownbey & Ownbey* 1443 (MIN, US); 38.7 miles e. of Sombrerete on road to Fresnillo, *Ownbey & Ownbey* 2035 (MIN).

3b. Argemone ochroleuca Sweet subsp. **stenopetala** (Prain) G. B. Ownb., comb. & stat. nov.

A. intermedia var. *stenopetala* Prain, in Journ. Bot. 33: 364. 1895; Fedde, in Pflanzenr. 4 (104): 282. 1909; not *A. intermedia* Sweet.

A. stenopetala Rose, in Contr. U. S. Nat. Herb. 8: 27. 1903.

Annual; leaves deeply lobed, the sinuses broad; buds oblong, small, the body 4-6 mm. wide, 8-12 mm. long, the sepal horns 5-8 mm. long including the slender terminal spine; flowers 3-5 cm. in diameter; petals pale lemon-yellow, narrowly elliptical, about 3 times as long as broad; stamens about 20-30; style in fruit about 1 mm. long; capsules 3-5-carpellate, the width, excluding the spines, 10-18 mm., the length, including the stigma, 20-40 mm., the armature consisting of larger spines intermixed with smaller spines and prickles, the larger spines 6-9 mm. long; longest dimension of seeds 1.8-2.0 mm. (Ill.: Fig. 3, 1-3; Dist.: Fig. 5.)

Holotype: *C. G. Pringle* 43, from "Valley near Chihuahua," state of Chihuahua, Mexico, May 2 and 24, 1885 (Cosson herbarium, Paris, according to Prain, l.c., pp. 364, 365, not seen; isotypes, F, GH, ND, NY, RSA, US).

Habitat and distribution: Valleys and high plains, often in disturbed soil, at altitudes of 4500-6500 feet in its native area, northern Durango and southern Chihuahua. The records from the states of México and Michoaeán doubtless are introductions.

Flowering and fruiting dates: Evidently flowers in March and continues to flower through the summer and fall as local conditions permit; fruits are matured from about April 15 to Sept. 30, or later.

Prain, l.c., while denying *A. intermedia* var. *stenopetala* full specific rank, did so with great hesitancy, mainly through reluctance to further increase the number of proposed species of *Argemone* in the absence of a more extensive suite of specimens. Rose, l.c., who had seen Prain's variety in the field raised it to specific rank without stating any reasons. He reported this taxon as occurring with *A. ochroleuca* "from which it is difficult to distinguish it except by color of the flowers." I, too, have seen the two subspecies of *A. ochroleuca* growing together as roadside weeds in northern Durango, both doubtless locally introduced. It is mainly on the basis of field observations that I herewith propose the transfer of Prain's *A. intermedia* var. *stenopetala* to *A. ochroleuca* in the higher rank of subspecies. The two subspecies of *A. ochroleuca* are indistinguishable in the field on vegetative characteristics. It is only by observing the distinctive features of the buds, petals and capsules set forth above that their individuality is apparent. No intermediates were observed in the field and it is most doubtful if they occur at all. I would, however, postulate the origin of subsp. *stenopetala* directly from subsp. *ochroleuca* despite the presence in the latter of new features not present in the former and the evident incompatibility barrier between them in nature.

Specimens examined: MEXICO.

CHIHUAHUA

23 miles s.e. of Hidalgo del Parral on road to Durango, *Ownbey & Ownbey* 1850 (BM, CAS, COLO, F, GH, MEXU, MICH, MIN, NY, RM, RSA, UC, US); valley near Chihuahua, *Pringle* 43 (isotypes of *A. intermedia* var. *stenopetala* Prain, F, GH, ND, NY, RSA, US); vicinity of Chihuahua, alt. about 1300 m., *Palmer* 153 (F, GH, K, MO, NY, US); Chihuahua city, *Rose & Hough* 4206 (US).

DURANGO

41.5 miles s.e. of Hidalgo del Parral on road to Durango, *Ownbey & Ownbey* 1857 (ARIZ, BM, GH, K, MEXU, MICH, MIN, MO, NY, POM, SMU, TEX, UC, WIS, WS); Tepehuanes, *Palmer* 36 (F, GH, K, MO, NY, US).

México

Lechería, alt. 7400 ft., *Pringle* 11919 (F, GH, US).

Michoacán

Morelia, *Arsène s.n., in part,* (US).

4. Argemone **superba** G. B. Ownb., sp. nov.

Herba annua latice luteo. Caules plerumque solitarii, 3-10 dm. alti, sparse aculeati. Folia pinnatifida, superioribus minus pinnatifidis, subter in venis aculeata, supra subinermia. Alabastra subsphaerica, 12-16 mm. lata, 12-16 mm. longa, 4-12 aculeis in utroque sepalo. Sepalorum coruna inermia, teretia, 7-10 mm. longa. Flores 7-9 cm. diametro, petalis luteis, staminibus circa 150, filamentis pallide flavis, stigmatis lobis aliquantum sinuatis post anthesim. Capsulae 3-5-carpellatae, late ellipticae, crasse spinescentes. Semina non visa.

Annual with bright yellow latex; stems mostly one from the base, 3-10 dm. tall, widely branched, distantly prickly; leaves very glaucous, the blue lines over the veins pronounced, the lower ones lobed to four-fifths the distance to the midrib, the upper ones less deeply lobed, the lobes broadly oblong with acute spine-tipped marginal teeth, the sinuses narrower than the lobes, the lower surfaces of the leaves stoutly and distantly prickly on the main veins, the upper surfaces very sparingly and weakly prickly on the main veins or smooth; buds subspherical, the body 12-16 mm. broad, 12-16 mm. long, with about 4-12 prickles on each sepal, the sepal horns smooth, terete, spreading, 7-10 mm. long including the terminal spine; flowers 7-9 cm. across, closely subtended by 1-2 foliar bracts; petals bright yellow, the outer suborbicular, the inner broadly obovate-obcuneate, the outer margins minutely erose; stamens numerous, about 150, the filaments pale yellow, the anthers yellow, equalling or slightly exceeding the stigma at anthesis; stigma purple, about 2.5-3.0 mm. wide and 2-3 mm. high, the lobes usually somewhat sinuate, especially after anthesis, more or less appressed to the style at anthesis; style very short, to about 0.5 mm. long in fruit; capsules 4-5-carpellate, broadly elliptical, the mature size unknown, but within the usual range for *Argemone*, armed with stout well-spaced, even-sized spines plus a few lesser spines or prickles, the capsular surface clearly visible; seeds not seen. (Ill.: Fig. 4, 1; Dist.: Fig. 5.)

Holotype: *G. B. Ownbey & F. Ownbey* 2044, collected 13.3 miles northwest of Ciudad del Maíz, San Luis Potosí, Mexico, in deep alluvial soil of road ditch, chaparral province, Oct. 25, 1953 (MIN; isotypes, BM, CAS, F, GH, MEXU, MICH, MIN, MO, NY, UC, US).

Habitat and distribution: Chaparral province, at altitudes of about 4500-6000 feet, southern San Luis Potosí west of the Sierra Madre Oriental.

Flowering and fruiting dates: During summer and fall months.

A. superba is closely allied to *A. aenea* and should possibly be considered a subspecies thereof. They differ in the generally more nearly spherical, less prickly, smaller buds of *A. superba* and the consistently pure yellow petals and lemon yellow filaments of *A. superba* as opposed to the usually golden yellow or bronze petals and uniformly red filaments of *A. aenea*. The stigma of *A. superba* evidences a lesser tendency toward sinuate lobes than *A. aenea* and is generally smaller. Finally, the capsules of *A. superba* are generally less closely armed than those of *A. aenea*. Distributionally the two taxa are entirely allopatric, the distribution of *A. superba* being southward and westward of *A. aenea* and separated by the

FIG. 4. 1. *A. superba.* Habit × 1. Isotype, *Ownbey & Ownbey* 2044 (MIN). 2-5. *A. aenea.* 2. Capsules × 1. *Ownbey & Ownbey* 1623 (MIN). 3. Stigma × 3. Cult. from seed of *Ownbey & Ownbey* 1409 (MIN). 4. Sepal × 1. Same as 3. 5. Bud × 1. Isotype, *Pringle* 8321 (UC).

Sierra Madre Oriental. Because of its yellow petals, *A. superba* might also be confused with *A. mexicana* or *A. ochroleuca*. It is readily separated from both of these species by its larger flowers and more numerous stamens.

Specimens examined: MEXICO.

San Luis Potosí

13.3 miles n.w. of Ciudad del Maíz, *Ownbey & Ownbey* 2044 (MIN, holotype of *A. superba* Ownb.; isotypes, BM, CAS, F, GH, MEXU, MICH, MIN, MO, NY, UC, US); Río Verde, *Palmer* 57, *in part* (GH, NY, US).

5. Argemone **aenea** G. B. Ownb., sp. nov.

A. mexicana Fedde, in Pflanzenr. 4 (104): 275. 1909, as to *Pringle* 8321; not *A. mexicana* L.

A. platyceras Fedde, l.c., p. 283, in small part; not *A. platyceras* L. & O.

Herba annua, biennis, aut diurnitate brevi perennis, latice flavo. Caules 3-8 (-10) dm. alti, sparse aculeati. Folia profunde pinnatifida glauca. Alabastra elliptico-oblonga, 12-16 mm. lata, 15-20 (-24) mm. longa, moderate aculeata. Sepalorum cornua teretia, 7-12 (-14) mm. longa. Flores 8-10 (7-12) cm. lati, petalis flavis vel aureis vel aeneis, staminibus circa 150, filamentis rubris aut purpureis, stigmatis lobis inter anthesim sinuatis. Capsulae 4-5-carpellatae, anguste ellipticae vel elliptico-oblongae, spinis robustis magnitudine inaequalibus. Semina circa 1.5-1.7 mm. longa.

Annual, biennial or short-lived perennial with bright yellow latex; stems 1-few, 3-8 (-10) dm. tall, moderately branched, sparingly to quite evidently prickly with usually slender, perpendicular or visibly reflexed prickles; leaves glaucous, the veins prominently blue lined, the lower ones pinnatifid, the middle and upper ones sometimes less deeply cut, the lobes oblong, with acute, prickle-tipped marginal teeth, the sinuses rectangular, broad, the leaf surfaces somewhat prickly on the veins below, smooth or very sparingly prickly on the veins above; buds at flowering time elliptic-oblong, the body 12-16 mm. broad, 15-20 (-24) mm. long, moderately prickly, the sepal horns approximately round in cross section, 7-12 (-14) mm. long, smooth or with a few prickles on the herbaceous base, spine-tipped; flowers usually 8-10 (7-12) cm. broad, usually closely subtended by 1-2 foliar bracts; petals yellow to golden or bronze, sub-orbicular to very broadly obovate-obcuneate, the outer margins erose; stamens about 150, the filaments red or purplish, the anthers purplish-yellow, the stamens and ovary sub-equal at flowering time; stigma purple, 3-6 mm. wide, about 2-3 mm. high, the lobes characteristically sinuate; capsules 4-5-carpellate, narrowly elliptical to elliptic-oblong, the width, exclusive of spines, 12-16 mm., the length, including the stigma, 25-35 mm., coarsely spiny, the larger spines interspersed with smaller ones, the longest spines usually to about 8 mm. long, the capsular surface clearly visible through the armature; seeds 1.5-1.7 mm. long. (Ill.: Fig. 4, 2-5; Dist.: Fig. 5.)

Holotype: *C. G. Pringle* 8321, collected in the Río Grande Valley near Díaz, alt. 700 ft., Coahuila, Mexico, April 20, 1900 (US; isotypes, F, GH, MEXU, MIN, MO, ND, NY, POM, RM, UC, US).

Habitat and distribution: Apparently native to the dry plains, low hills and drainages of southern and western Texas and northeastern Mexico; now also a weed along roadsides, in fields, pastures and waste lots of the same area. It evidently tolerates a wide range of soil types. It is found at elevations of near sea level in the east to about 4500 ft. in the west.

Flowering and fruiting dates: First flowers appear in mid-February; flowers may continue to appear in individual plants during the spring,

summer and autumn. First fruits mature beginning about March 15 and continue to mature until autumn as local conditions permit.

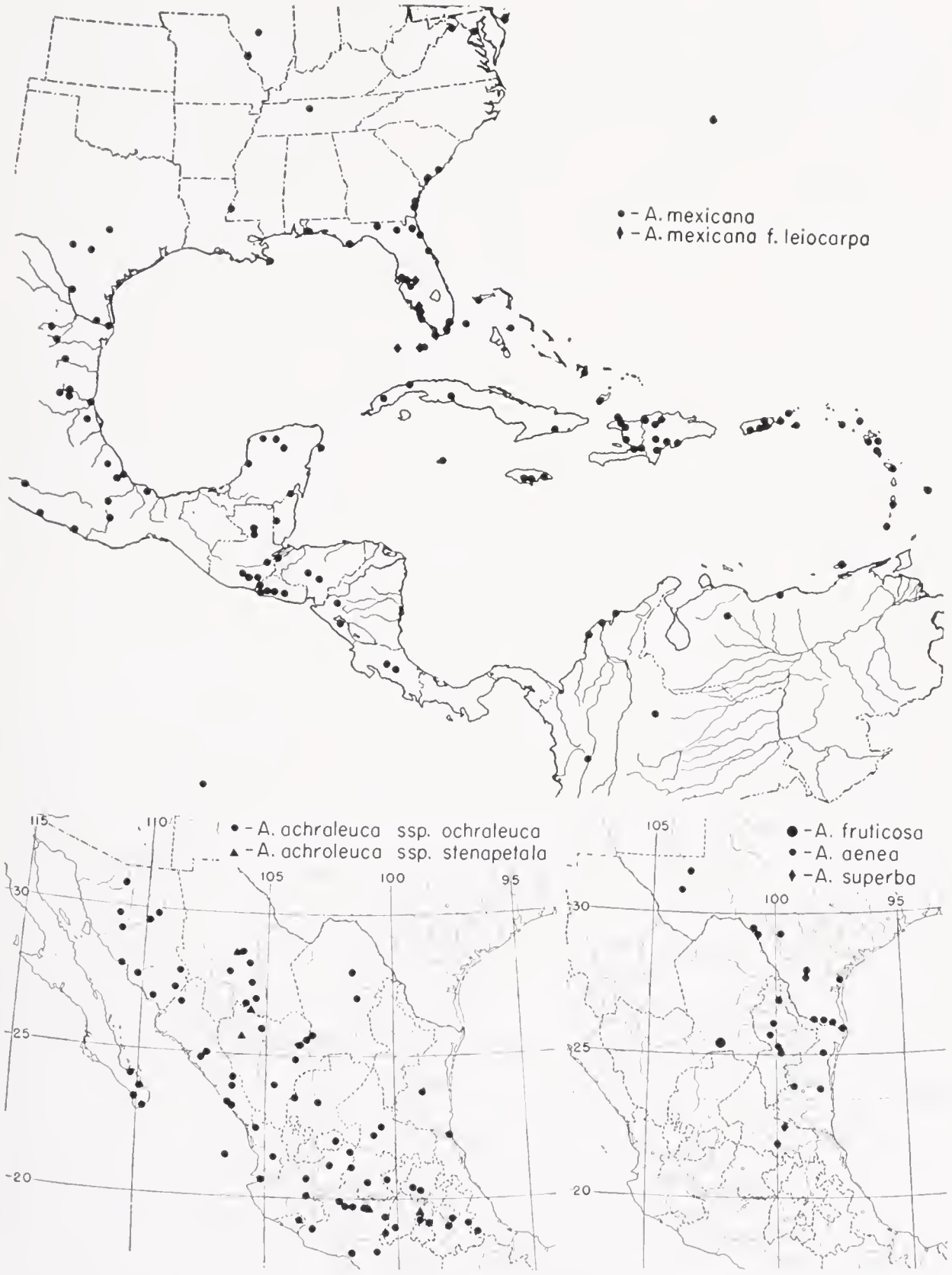

FIG. 5. Geographical distributions of species and subspecies as indicated.

A. aenea is closely related to *A. superba*. The differences between the two are set forth under the latter species. In herbaria it has usually passed as either *A. mexicana* or *A. ochroleuca* because of its flower color. It may be readily distinguished from these two species on the basis of its larger flowers, larger, more prickly buds, more numerous stamens, red or purplish filaments and usually sinuate stigmatic lobes. Superficially, if one does not take flower color into account, the resemblance of *A. aenea* to *A. sanguinea* is much closer. The only consistent morphological difference seems to lie in the stigmatic lobes which are sinuate in the former species and not sinuate in the latter species. Although these two species occur together in southern Texas, I have detected no conclusive evidence of natural hybridization between them, at least between *A. aenea* and the tetraploid form of *A. sanguinea*. One specimen, *Ownbey & Ownbey* 1627c (MIN) appears to be of hybrid origin. It was collected 1.4 miles s.e. of Garciasville, Starr Co., Texas. Two putative hybrids with salmon-pink flowers were seen at this locality growing with the presumed parents. All plants appeared fertile but seeds of one of the hybrids did not germinate when planted. It seems probable, at this writing, that hybridization between *A. aenea* and *A. sanguinea* is rare, if it occurs at all.

Specimens examined: UNITED STATES.

TEXAS

Cameron Co.: La Feria, alt. 50 ft., *Runyon* 609 (US); Brownsville, *York s.n.* (TEX). Duval Co.: 0.5 mile n. of Freer, *Cory* 55313 (SMU, US). Hidalgo Co.: 2.8 miles e. of Edinburg, *Ownbey & Ownbey* 1616 (CAS, F, GH, K, MIN, NY, RM, SMU, TEX, UC, US); 9.4 miles e. of Hidalgo, *Ownbey & Ownbey* 1623 (GH, MIN, SMU, TEX, US); Weslaco, alt. 20 m., *Runyon* 1616 (US). Jeff Davis Co.: Phantom Lake, *Cory* 18316 (GH); lower Little Aguja Canyon, Espy ranch, alt. 4800 ft., *Warnock* 8040 (SMU, very aberrant); Madera Canyon below Madera Springs, *Whitehouse* 11814 (SMU). Maverick Co.: Del Rio to Eagle Pass, *Hanson* 537 (MO, NY, US); 7.7 miles n.w. of Quemado, *Ownbey & Ownbey* 1632 (GH, MIN, NY, RSA, SMU, TEX, UC, US). McMullen Co.: 17¼ miles s. of Tilden, *Cory* 55326 (SMU). Nueces Co.: Corpus Christi, *Nealley s.n.* (F). Reeves Co.: Toyah Creek at Balmorhea, *Cory* 52241 (SMU); plains w. of Pecos, *Earle & Tracy* 423 (NY); n. edge of Davis Mts., 1 mile e. of intersection of Hwys. 80 & 290, *Waterfall* 4394 (CAS, GH, MO, NY). Starr Co.: 1.4 miles s.e. of Garciasville, *Ownbey & Ownbey* 1627b (MIN). Uvalde Co.: 10.5 miles w. of Uvalde, *Ownbey & Ownbey* 1643 (C, CAS, F, GH, K, KSC, MIN, NY, SMU, TEX, UC, US). Val Verde Co.: 11 miles s.e. of Del Rio, *Ownbey & Ownbey* 1633 (MIN, SMU); Del Rio, *Palmer* 13586 (MO, US).

MEXICO.

COAHUILA

Río Grande Valley near Díaz, alt. 700 ft., *Pringle* 8321 (US, holotype of *A. aenea* Ownb.; isotypes, F, GH, MEXU, MIN, MO, ND, NY, POM, RM, UC, US).

NUEVO LEÓN.

Monterrey, alt. 1750 ft., *Fisher s.n.*, 138 (MO, US); 38 miles s. of Nuevo Laredo on road to Monterrey, *Frye & Frye* 2359 (DS, GH, MO, NY, RSA, UC, US); Montemorelos, *Nelson* 6099, 6699 (GH, US); 6.2 miles n. of Ciénega de Flores, *Ownbey & Ownbey* 1403

(GH, K, MEXU, MIN); 17.5 miles n.w. of Montemorelos, *Ownbey & Ownbey* 1409 (GH, MEXU, MIN); San Juan, near Monterrey, *Prinkle* 11358 (US); Mt. Mitras, alt. 1645 ft., *Roybal* 17 (TEX); Cerro de la Silla, near Monterrey, alt. 1700 ft., *White* 1506 (GH).

TAMAULIPAS

54 miles s. of Matamoros, *Meyer & Rogers* 2479 (MIN, MO); Soto la Marina, *Nelson* 6053, 6653 (F, NY, US); 16.3 miles n.w. of C. Victoria, *Ownbey & Ownbey* 1412 (MIN); near Matamoros, *Tharp* 1789 (TEX, US).

6. ARGEMONE **aurantiaca** G. B. Ownb., sp. nov.

A. planchonii Prain, in Journ. Bot. 33: 369. 1895, as to Texas, provisional name having no taxonomic standing.

A. platyceras var. *typica* Prain, l.c., p. 367, in small part; not *A. platyceras* L. & O.

A. platyceras var. *typica* Prain "state" δ Prain, l.c., p. 369, excluding *Fendler* 16; not *A. platyceras* L. & O.

A. platyceras Small, Fl. s.e. U. S., p. 462. 1903, as to Texas distribution, in part; not *A. platyceras* L. & O.

Herba annua aut biennis latice rufo-aurantiaco. Caules usque ad 8 dm. alti, late ramosi, omnino moderate vel dense aculeati, aculeis longis tenuibus perpendicularibus. Folia oblanceolata, inferioribus profunde lobatis lobis oblongis, superioribus repande lobatis ovatis amplexicaulibusque, in venis principalibus aculeata praecipue subter, aliquando utrinque inter venas sparse aculeata. Alabastra oblonga, 14-18 mm. lata, 18-25 mm. longa, aculeata. Sepalorum cornua angulata aut in sectione transverse planata, 8-12 mm. longa, aculeata. Flores foliis 1-2 reductis subtensae, 8-12 cm. diametro, petalis albis, staminibus 150 vel plus. Capsulae 5-6-carpellatae, ovatae, 15-25 mm. latae, 40-50 mm. longae stigmate includenti, spinis longis saepe ramosis herbaceis ad 35 mm. longis et aculeis multis et secundariis dense obsidentes, superficie capsulari aculeis parvis simplicibus inter spinas munita, partim obscurata. Semina 2.5-3.0 mm. longa.

Annual or biennial with reddish-orange latex; stems usually 1 from the base, to about 8 dm. tall, stout, widely branched upward, the primary branches few in number and surpassing the main axis, the plant at maturity more or less flat-topped, the stems moderately to copiously prickly throughout with long, slender, perpendicular prickles; leaves bluish, the basal and lower cauline oblanceolate, deeply lobed to four-fifths the distance to the midrib, the lobes oblong, the leaves progressively elliptical to ovate upward, less deeply lobed, the uppermost ones only shallowly lobed and often clasping the stem, all the leaves with secondary, angular lobes and points marginally, the points terminated by a usually weak spine or prickle, the leaves sparingly to copiously prickly on the veins, especially below, with slender prickles and also sometimes very sparingly prickly on the surfaces between the larger veins, especially below; buds oblong, often very large, the body 14-18 mm. broad, 18-25 mm. long, sparingly to densely prickly, the larger prickles sometimes compound, the sepal horns angular, often dorsi-ventrally flattened, usually 8-12 mm. long, prickly to the indurated apical spine; flowers closely subtended by 1-2 reduced leaves, 8-12 cm. in diameter; petals white; stamens numerous, 150 or more, the filaments pale yellow, the anthers yellow; stigma purple, 3.5-5.0 mm. wide, 2.5-3.5 mm. high, 5-6 lobed; capsules 5-6-carpellate, ovate, the body, exclusive of armature, 15-25 mm. broad, 40-50 mm. long, including the stigma, densely covered with long, herbaceous, erect or reflexed spines, these to 35 mm. long, often branched, provided with numerous secondary prickles for three-fourths their length and terminated by a slender, indurated point, the capsule also provided with small, simple prickles arising between the large spines, the capsular surface partially but not completely obscured; seeds 2.5-3.0 mm. long. (Ill.: Fig. 6, 1-5; Dist.: Fig. 13.)

Holotype: *Gerald B. Ownbey & Findley Ownbey* 1397, from 6.3 miles

northeast of San Marcos, U. S. Highway 81, Hays Co., Texas, July 12, 1950 (MIN; isotypes, GH, K, MIN, MO, SMU, US).

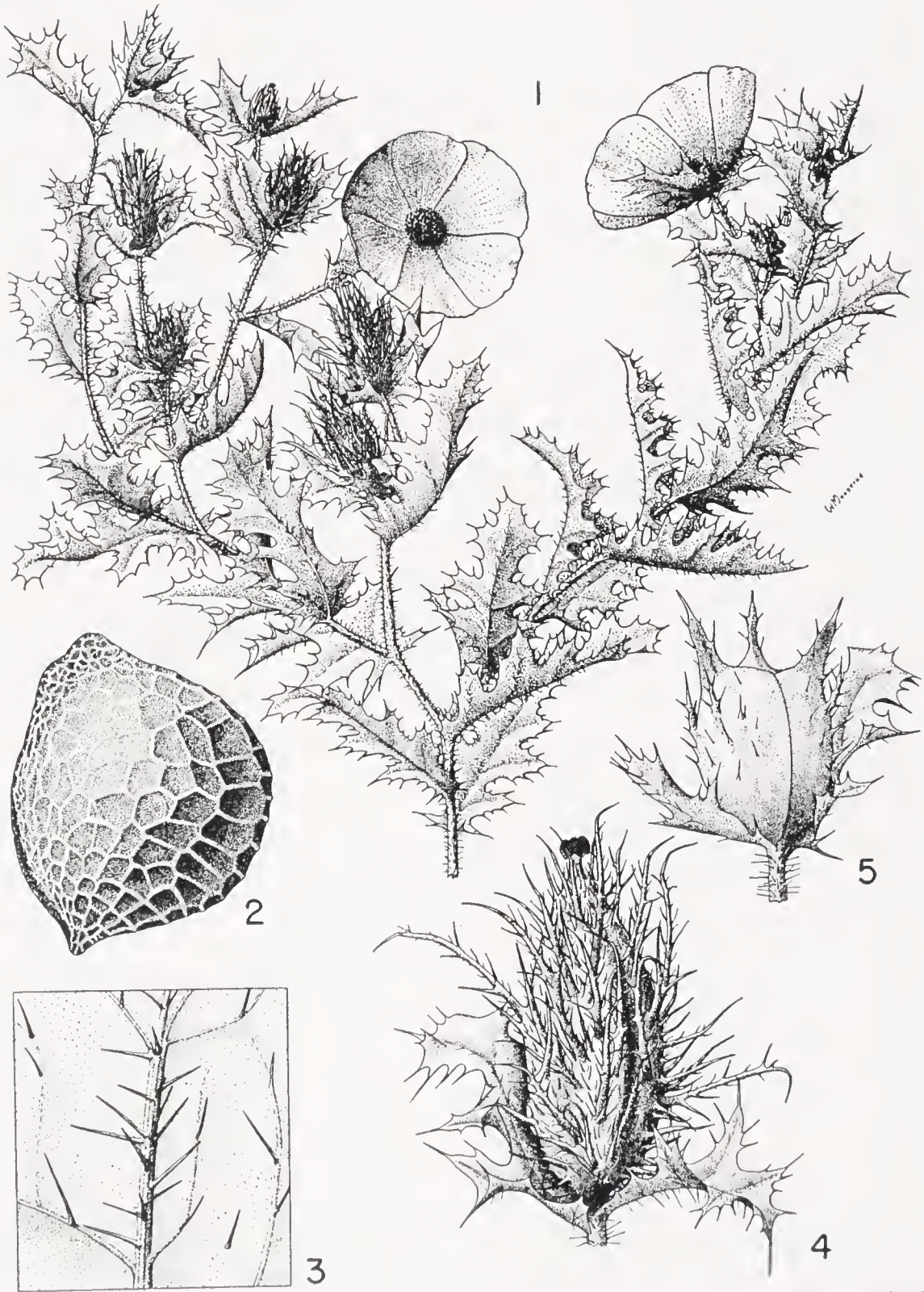

FIG. 6. *A. aurantiaca*. 1. Habit × 3/8. Holotype, *Ownbey & Ownbey* 1397 (MIN). 2. Seed × 15. *Ownbey & Ownbey* 1394a (MIN). 3. Leaf, under surface along midvein, × 4. Cult. from seeds of *Ownbey & Ownbey* 1394a (MIN). 4. Capsule × 1. Isotype, *Ownbey & Ownbey* 1397 (MIN). 5. Bud × 1. *Smith* 1154 (TEX).

Habitat and distribution: Fields and pastures, hilly terrain, often rocky, sandy soil, south-central Texas in the region of the Balcones Escarpment of the Edwards Plateau and northward along the transition zone between the lowland plains and the plateau regions to the west; introduced locally westward.

Flowering and fruiting dates: Flowering begins about April 1-15 and continues as conditions permit through the summer to August; fruits begin to ripen about May 15-30 and continue to ripen until autumn.

This species regularly has been considered a component either of *A. platyceras* L. & O. or of *A. hispida* Gray when the latter was given specific rank. Dr. David Prain first noted its distinctive capsule armature (to some degree shared only by *A. squarrosa*) and treated it as "state" ♂ of *A. platyceras* var. *typica* in his monograph of the genus. He provisionally suggested calling the species *A. Planchonii*, but the name was not accepted by him and has not since been validly published. The name may, therefore, be rejected under Article 33 of the International Code of Botanical Nomenclature, 1956 edition. I prefer to call attention to the unique latex color of this species and for this reason am naming it *A. aurantiaca*. Prain erred in placing fruiting specimens of *Fendler* 16, from the prairies, upper spring of the Cimarron, with his Texas material of this "state." This portion of *Fendler* 16 belong with *A. squarrosa* Greene subsp. *squarrosa*.

A. aurantiaca differs from *A. hispida* in the absence of hispidity on the stem and leaf surfaces and in the coarse, often branched spines of the capsules. It differs similarly from *A. platyceras* in capsule characters. The plants are coarser throughout than either *A. hispida* or *A. platyceras*. *A. aurantiaca* resembles *A. squarrosa* Greene subsp. *squarrosa* in many respects, but may be readily distinguished on the basis of the uniform hispidity of stems and leaves and shorter capsular spines of the latter. Cytologically, *A. aurantiaca* with its diploid chromosome number of 84 differs from *A. platyceras*, which has a diploid number of 28, and *A. squarrosa* subsp. *squarrosa*, which has a diploid number of about 112. The chromosome number of *A. hispida* has not yet been determined.

Specimens examined: UNITED STATES.

TEXAS

Bell Co.: Temple, *Killough* 17 (US). Bexar Co.: San Antonio, *Mr. & Mrs. J. Clemens* 795 (MO, RM); no locality, *Jermy s.n.* (MO, NY). Comal Co.: around Bracken, *Groth* 45 (CAS, F, GH, NY, US). Gillespie Co.: Harper, *Whitehouse* 702 (NY). Hays Co.: 6.3 miles n.e. of San Marcos, *Ownbey & Ownbey* 1397 (MIN, holotype of *A. aurantiaca* Ownb.; isotypes, GH, K, MIN, MO, SMU, US). Kerr Co.: no locality, *Whitehouse s.n.* (TEX). McLennan Co.: 2.4 miles s.-s.e. of Crawford, *Shinners* 14978 (SMU). Medina Co.: D'Harris, *Ownbey & Ownbey* 1400 (MIN). Taylor Co.: near Abilene along R.R., *Tolstead* 7466 (SMU, TEX, UC). Travis Co.: rim of rocks, edge of caliche pit, Zilker Park, *Barkley & Warnock* 46265 (RSA, TEX, US); 5.3 miles s.e. of Austin, *Ownbey & Ownbey* 1394a (MIN, TEX, UC). Uvalde Co.: 2.9 miles w. of

Sabinal, *Ownbey & Ownbey* 1646 (MIN). County uncertain: no locality, *Drummond* 9 (GH); between Texas and New Mexico, ex *Torrey s.n.* (GH).

7. Argemone **echinata** G. B. Ownb., sp. nov.

A. platyceras Wats., in Proc. Am. Acad. 17: 318. 1882, as to *Palmer* 19; Hemsl., Biol. Cent. Am., Bot. 4: 4. 1886, as to *Palmer* 19; Fedde, in Pflanzenr. 4 (104): 283. 1909, in small part; not *A. platyceras* L. & O.

A. platyceras var. *typica* Prain, in Journ. Bot. 33: 367. 1895, in small part; not *A. platyceras* L. & O.

A. platyceras var. *typica* Prain "state" β Prain, l.c., p. 368, in part; not *A. platyceras* L. & O.

A. hispida Rose, in Contr. U. S. Nat. Herb. 8: 26. 1903, as to cited specimens; not *A. hispida* Gray.

A. platyceras var. *hispida* Fedde, in Pflanzenr. 4 (104): 285. 1909, in very small part; not *A. platyceras* L. & O.; not *A. hispida* Gray.

Herba perennis. Caules solitarii vel plures, 3.5-5.5 dm. alti, omnino conspicue et aliquantulum dense aculeati, aculeis tenuibus rigidis perpendicularibus magnitudine inaequalibus. Folia profunde pinnatifida lobis oblongis, lobis secundariis lanceolatis, lamina sparse aculeata vel aliquando densius aculeato-hispida utrinque inter venas principales. Alabastra elliptico-oblonga moderate aculeata. Sepalorum cornua teretia, circa 10 mm. longa, in parte basali herbacea aculeata. Flores 1-2 bracteis foliaribus subtensi, 6-10 cm. diametro, staminibus circa 100. Capsulae 3-4-carpellatae, late oblongae vel ellipticae, 10-14 mm. latae, 20-35 mm. longae, superficie spinis multis et erectis aut patentibus armatae, spinis maximis 9-11 mm. longis et ipsis aliquando aculeatis, superficie capsulari quoque spinis parvis et aculeis armatae. Semina circa 2 mm. longa.

Perennial, the latex color unknown; stems 1-several from the base, usually 3.5-5.5 dm. tall, widely branched, the branches equalling or surpassing the primary axis, the plant at maturity more or less flat-topped, the stems conspicuously and rather closely prickly throughout with very uneven-sized, slender, rigid, perpendicular prickles; leaves bluish, the upper ones not conspicuously clasping, the blades usually deeply pinnatifid to three-fourths or more of the distance to the midrib, the sinuses broad, the lobes oblong and with lanceolate secondary lobes, each of which is terminated by a stout spine, the leaves prickly on the veins below and above, and from sparsely prickly to sometimes rather closely aculeate-hispid on the surfaces between the larger veins both below and above; buds medium-sized, elliptic-oblong, the body 8-10 mm. broad, 14-18 mm. long, moderately prickly, the sepal horns terete, about 10 mm. long, prickly on the herbaceous basal portion, rarely also on the stout, indurated, terminal spine; flowers closely subtended by 1-2 foliar bracts, 6-10 cm. in diameter; petals white; stamens about 100, the filaments pale yellow, the anthers deep yellow; stigma purple, 2.5-3.5 mm. wide, 1.5-2.5 mm. high, 3-4-lobed; capsules 3-4-carpellate, broadly oblong to elliptical, the body, excluding armature, 10-14 mm. broad, the length, including the stigma, 20-35 mm., armed with numerous erect or spreading spines, the larger spines usually 9-11 mm. long and indurated to near the base, these occasionally with secondary prickles on the herbaceous basal portion, the capsule also armed with small spines and prickles, the surface obscured, but still visible; seeds about 2 mm. long. (Ill.: Fig. 7, 1-5; Dist.: Fig. 13.)

Holotype: *Dr. Edward Palmer* 208, from the vicinity of Satillo, Coahuila, Mexico, June, 1898 (US; isotypes, F, GH, MO, NY, UC).

Habitat and distribution: Flat valley floors and playas, often in deep, clay soil, eastern Coahuila, northern San Luis Potosí and western Nuevo León, Mexico, at elevations of 4500 to 6500 feet to the south, much lower to the north.

Flowering and fruiting dates: Flowers appear about May 1 and, condi-

tions permitting, continue into August; first fruits mature in early June and fruits continue to mature to September.

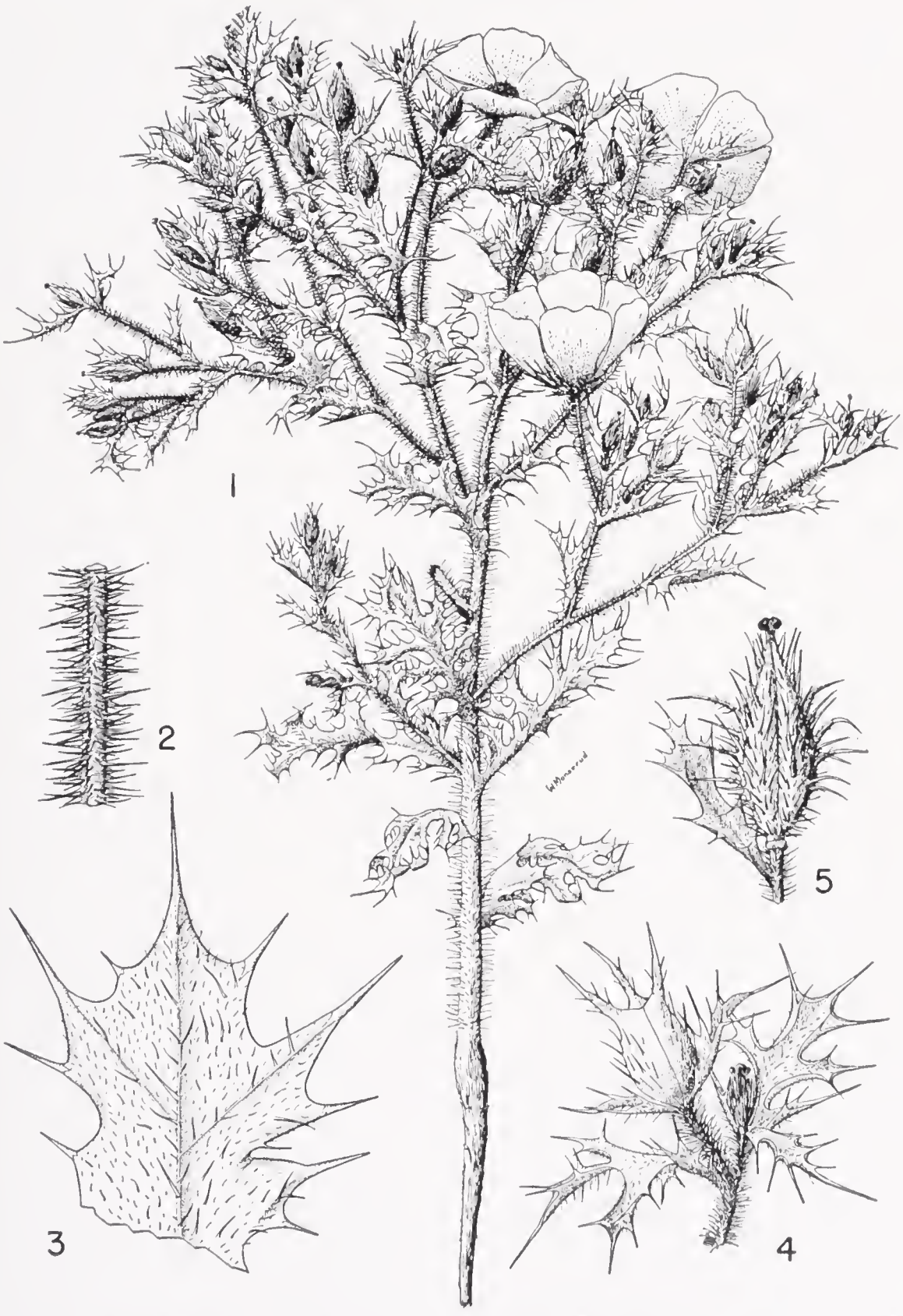

FIG. 7. *A. echinata*. 1. Habit × 3/8. Topotype, *Ownbey & Ownbey* 1408 (MIN). 2. Main stem × 1. *Stanford et al.* 280 (UC). 3. Leaf lobe, upper surface × 3. Same as 2. 4. Bud × 1. *Stanford et al.* 280 (NY). 5. Capsule × 1. Isotype, *Palmer* 208 (GH).

The distinguishing characters of *A. echinata* lie in its low stature, conspicuous prickliness of the stems, lanceolate ultimate leaf lobes and the more or less aculeate-hispid leaf surfaces. The sepal horns appear to be uniformly round in cross-section. Finally, the capsules are rather densely armed with large prickles interspersed with uneven-sized smaller ones.

A. echinata is found in its most typical state in southeastern Coahuila and adjacent Nuevo León and San Luis Potosí. Specimens collected to the north, e.g., at Múzquiz, Sabinas and Díaz (not located), at low elevations, are quite atypical, particularly in their less dense prickliness; those from Díaz, *Pringle* 8294, are coarser, more open in habit, and have larger flowers. It seems very probable that the Díaz specimens have been influenced by hybridization with another species in this area.

Specimens of *A. echinata* have been placed by previous students of the genus in either *A. platyceras* L. & O. or *A. hispida* Gray. Prain, in his monograph of *Argemone*, cites *Palmer* 19 under *A. platyceras* var. *typica* and makes it a part of "state" β of this variety. Fedde in his later monograph also cites *Palmer* 19 under *A. platyceras* proper. In treating the Mexican species of *Argemone*, Rose cites *Palmer* 19 and *Palmer* 208 as *A. hispida*. From *A. hispida* Gray, *A. echinata* differs in having stouter, more widely spaced capsule spines, in the more lanceolate ultimate leaf lobes which are tipped by a stouter spine, and in the absence of crisped indumentum on the leaf surfaces and stem. *A. echinata* differs from *A. platyceras* L. & O. in many ways, especially in the stouter capsule armature, and smaller buds, the sepal horns being round rather than laterally flattened in cross-section. In general aspect the plants are rather similar to *A. squarrosa* Greene subsp. *squarrosa*, but are smaller in stature and in all their parts.

The somatic chromosome number, 28, is the same as in *A. platyceras*, but differs from *A. squarrosa* subsp. *squarrosa* which apparently is an octaploid. The chromosome number of *A. hispida* is unknown. Other species of this alliance are all diploids with 28 somatic chromosomes except *A. aurantiaca* which apparently is a hexaploid.

Specimens examined: MEXICO.

COAHUILA

Valley near Buenavista, *Gregg s.n.* (MO, NY); valley near Saltillo, *Gregg* 95 (MO); Múzquiz, *Marsh* 20 (TEX); Sabinas, *Nelson* 6206, 6806 (F, NY, US); 2.1 miles n. of Saltillo on road to Monterrey, *Ownbey & Ownbey* 1408 (K, MEXU, MICH, MIN, SMU); Saltillo, *Palmer* 19 (GH, US); vicinity of Saltillo, *Palmer* 208 (US, holotype of *A. echinata* Ownb.; isotypes, F, GH, MO, NY, UC); Río Grande Valley near Díaz, alt. 700 ft., *Pringle* 8294 (F, GH, MEXU, MIN, MO, ND, NY, POM, RM, UC, US); Fraile, 59 km. s. of Saltillo, alt. 1967 m., *Stanford, Retherford & Northcraft* 280 (DS, MEXU, MO, NY, UC).

Nuevo León

Hacienda Pablillo, Galeana, *Taylor* 109 (DS, F, MO, RSA, TEX).

San Luis Potosí

Sierra de Catorce, *Rodriguez* 8 (F, US).

8. Argemone squarrosa Greene, in Pittonia 4: 68. 1899.

Perennial with yellow latex; stems 1-several from the base, widely branched, more or less flat-topped at maturity, very densely and copiously prickly with uneven-sized prickles to moderately prickly with rather even-sized prickles; basal leaves deeply lobed, the segments oblong, the middle leaves more shallowly lobed, the uppermost distinctly clasping the stem, the margins acutely dentate, each tooth terminated by a rigid prickle, the leaf surfaces closely to moderately prickly on the main veins beneath, less so to smooth on the main veins above, the areas between the larger veins conspicuously and densely minutely aculeate-hispid to smooth above and below; buds subspherical to oblong, the body 15-20 mm. broad, 16-25 mm. long, sparingly to moderately prickly, the sepal horns more or less angular in cross-section, 8-18 mm. long, prickly, terminated by a stout, indurated spine; flowers closely subtended by 1-2 reduced leaves, 8-12 cm. in diameter; petals white; stamens 150 or more, the filaments pale yellow, the anthers yellow; stigma purple, 3-5 mm. broad, 2.0-3.5 mm. high, 4-5 lobed; capsules 4-5-carpellate, elliptical, oblong, or lance-ovate, the width, exclusive of armature, 10-18 mm., the length, including the stigma, 25-50 mm., densely to sparsely covered with basally herbaceous, spreading or reflexed spines, the largest ones usually 8-15 mm. long, these more or less prickly, the capsular surface also densely to sparingly aculeate between the large spines; seeds to 2.5 mm. long.

Lectotype: *Josephine Skehan* 79, from near Gray (now Capitan), altitude nearly 6000 ft., Lincoln Co., New Mexico, August 1898 (US; isotypes, GH, MIN, MO, ND, NY, POM, RM, UC).

Key to the subspecies:

1. Surfaces of capsules densely aculeate as well as spinescent; leaf surfaces prickly on the larger veins of both surfaces and more or less densely aculeate-hispid between the larger veins; s.e. Colorado, w. Kansas & Oklahoma, n.e. & s.e. New Mexico ..... 8a. *A. squarrosa* subsp. *squarrosa*

1. Surfaces of capsules moderately to sparingly aculeate as well as spinescent; leaf surfaces prickly on the larger veins at least beneath and smooth or very sparingly aculeate-hispid between the larger veins; w. Texas & s.e. New Mexico ..... 8b. *A. squarrosa* subsp. *glabrata*

8a. Argemone squarrosa Greene subsp. squarrosa

A. squarrosa Greene, in Pittonia 4: 68. 1899; Fedde, in Pflanzenr. 4 (104): 287, 274, fig. 36Q. 1909; Woot. & Standl., Fl. N. Mex., in Contr. U. S. Nat. Herb. 19: 261. 1915; Rydb., Fl. R. Mts., p. 318. 1917; Rydb., Fl. Pr. & Pl., p. 353. 1932; Gates, Fl. Kans., p. 156. 1940; Stevens, Kans. Wild Fl., p. 116. 1948.

A. hispida Gray, Pl. Fendl., in Mem. Am. Acad. 4: 5. 1849, as to description of fruits; Brit., Man., p. 439. 1901, in part; Small, Fl. s.e. U. S., p. 462. 1903, as to Kansas distribution; Britton & Brown, Ill. Fl., ed. 2, 2: 139. 1913, as to Kansas distribution; Rydb., Fl. R. Mts., p. 318. 1917, as to Kansas distribution; Gates, Fl. Kans., p. 156. 1940; Stevens, Kans. Wild Fl., p. 116. 1948; not *A. hispida* Gray.

A. platyceras var. *typica* Prain, in Journ. Bot. 33: 367. 1895, in small part; not *A. platyceras* L. & O.

A. platyceras var. *typica* Prain "state" δ Prain, l.c., p. 369, as to fruiting example of *Fendler* 16; not *A. platyceras* L. & O.

A. alba Hitch., in Contr. U. S. Nat. Herb. 3: 541. 1896; not *A. alba* Lestib.; not *A. alba* Raf.; not *A. alba* James.

A. platyceras Gray, Syn. Fl. N. Am. 1 (1): 88. 1895, as to specimens with capsular spines "sometimes herbaceous below and again prickly down their sides"; Fedde, in Pflanzenr. 4 (104): 283. 1909, in small part; Stemen & Myers, Okla. Fl., p. 162. 1937; not *A. platyceras* L. & O.

Plants perennial by crown sprouts; latex pale yellow; stems 1-several from the base, ordinarily 3-5 (-8) dm. tall, widely branched toward the top, the primary branches few in number and surpassing the main axis, the stems at maturity more or less flat-topped, conspicuously, often densely prickly throughout, the larger prickles intergrading gradually into minute prickles; leaves bluish, the middle and upper cauline ones sessile, the uppermost ones clasping the stem, lobed, the lobes oblong, the sinuses shallow or to three-fourths or more the distance to the midrib, the lobes with lanceolate or deltoid secondary lobes, each terminated by a weak spine, the leaves prickly on the veins above and below and conspicuously, often densely minutely aculeate-hispid on the areas between the larger veins above and below; buds broadly oblong, the body 15-20 mm. broad, 20-25 mm. long, sparingly to moderately prickly, the sepal horns more or less angular in cross-section, dependent upon the amount of induration, 10-14 (-18) mm. long, prickly, terminated by a stout, indurated spine; flowers closely subtended by 1-2 reduced leaves, 8-12 cm. in diameter; petals white; stamens numerous, at least 150, the filaments pale yellow, the anthers yellow; stigma purple, 3.5-4.5 mm. wide, 2.5-3.5 mm. high, 4-5 lobed; mature capsules 4-5-carpellate, narrowly elliptical to ovate, the body, exclusive of armature, 10-18 mm. broad and 35-45 mm. long including the stigma, more or less densely covered with stout, spreading to reflexed spines, the larger spines usually 10-15 mm. long, herbaceous, provided with numerous secondary prickles for about one-half to three-fourths their length, sometimes branched, terminated by a stout, indurated point, the capsule also minutely aculeate, usually densely so, between the spines; seeds about 2.5 mm. long. (Ill.: Fig. 8, 1-3; Dist.: Fig. 13.)

Lectotype: That of the species.

Habitat and distribution: Prairies and foothills, deep, often sandy soils, western Kansas and Oklahoma, southeastern Colorado, northeastern and southeastern New Mexico, at altitudes of about 3300-6000 ft.

Flowering and fruiting dates: First flowers appear in late May and June; flowering continues through the summer and autumn until the middle of September; fruits mature from late July through September and early October.

A. squarrosa subsp. *squarrosa* appears to be closely allied to *A. hispida* with which it shares many features of gross aspect. The aculeate-hispid nature of the inter-vein surfaces of the leaves of subsp. *squarrosa* approaches that typical of *A. hispida*. This hispidity differs in being somewhat coarser in subsp. *squarrosa*. The capsular armature in *A. hispida* is fine, dense and simple; the much stouter and longer capsular spines of *A. squarrosa* subsp. *squarrosa* are sometimes branched, and are provided with secondary prickles along much of their length. Furthermore, the ultimate lobes of the leaves tend to be more lanceolate, and the terminal spines of the lobes longer and stouter in *A. squarrosa* subsp. *squarrosa*.

A. squarrosa subsp. *squarrosa* is similar to *A. aurantiaca* in stature, gross size of buds and capsules, and particularly in the armature of the

capsules. The primary spines in *A. aurantiaca* are, however, ordinarily somewhat longer and exhibit a stronger tendency toward branching than in *A. squarrosa* subsp. *squarrosa*. The two taxa differ markedly in the presence of inter-vein aculeate-hispid prickles in the latter subspecies and in the color of the latex, reddish-orange in *A. aurantiaca* and yellow in *A. squarrosa* subsp. *squarrosa*. The difference in somatic chromosome numbers between the two is also of importance, 84 in the former species and about 112 in the latter.

Although points of similarity of *A. squarrosa* subsp. *squarrosa* and other species of the complex exist, the present writer does not hesitate to accord the subspecies together with subsp. *glabrata* full specific rank.

The description of the fruits of *A. hispida* Gray, in the original diagnosis, was drawn from specimens of *A. squarrosa* subsp. *squarrosa*. With reference to the fruits, the original diagnosis of *A. hispida* reads: "The pod is covered with very strong spines, of which the larger are often branched, and also with smaller prickles and a hoary and bristly pubescence." The type collection of *A. hispida* is *Fendler* 16, from Santa Fe, New Mexico. All of Fendler's specimens from this locality are in bud and flower and are *A. hispida*. A fruiting specimen of *Fendler* 16 (MO), from "On Prairies, Upper spring of Cimaron, Aug. 27*th*, 1847" is *A. squarrosa* subsp. *squarrosa*. Gray also cites Fremont and Wislizenus as having procured *A. hispida*. *Wislizenus* 432 (MO), collected "on the Arkansas, Santa Fe road," in bud and flower, is *A. squarrosa* subsp. *squarrosa*. Fremont's collections, made enronte to California in 1845 (GH, US), which are in good fruit, are *A. squarrosa* subsp. *squarrosa*; however, a flowering and imperfectly fruiting specimen (GH), mounted with the Fremont collection is *A. hispida*. The original description of the fruits of *A. hispida* may have been drawn, in small part, from this latter specimen and to this extent the original description of the fruits of *A. hispida* may be correctly applied.

It appears that Greene took neither the material of *A. hispida* cited by Gray nor the original diagnosis of that species into account when he described *A. squarrosa*. He evidently based his description entirely upon Skehan's August, 1898, specimens from the village of Gray (now Capitan), Lincoln Co., New Mexico. In so doing, a number of specimens of the species from western Kansas and western Oklahoma, already extant in herbaria, were overlooked. *A squarrosa* subsp. *squarrosa* is still present at the type locality (*Ownbey & Ownbey* 1477).

Prain included fruiting specimens of *Fendler* 16 with his "state" δ of *A. platyceras* var. *typica*. It should be noted here that the central Texas material of this "state" is herein included in a new species *A. aurantiaca*.

Fruiting material of *Fendler* 16 as stated above, belongs with *A. squarrosa* subsp. *squarrosa*.

Specimens examined: UNITED STATES.

COLORADO

Baca Co.: 16.4 miles n. of Springfield (Hwy. 287), *Ownbey & Ownbey* 1705 (MIN). Bent Co.: Rule Creek, *Osterhout* 4106 (NY, RM); 4.6 miles s.e. of Las Animas (Hwy. 101), *Ownbey & Ownbey* 1668 (BM, CAS, COLO, GH, KSC, MICH, MIN, OKL, POM, RM, US, WS). Prowers Co.: 10.7 miles e. of Lamar, *Ownbey & Ownbey* 1670 (ARIZ, COLO, F, IA, ILL, K, MIN, NY, TEX, UC, UTC, US, WIS); 8.9 miles south of Lamar (Hwy. 287), *Ownbey & Ownbey* 1704 (MIN).

KANSAS

Clark Co.: no locality, *Hitchcock s.n.* (KSC). Gove Co.: no locality, *Hitchcock s.n.* (KSC). Gray Co.: no locality, *Hitchcock s.n.* (KSC). Hamilton Co.: no locality, *Hitchcock* 11 (GH, KSC, MO, NY, RM, US); 9.8 miles w. of Syracuse on road to Coolidge, *Ownbey & Ownbey* 1671 (COLO, GH, KSC, MIN, NY, OKL, RM, US); vicinity of Syracuse, *Rose & Fitch* 17022 (NY, US). Hodgeman Co., no locality, *Hitchcock s.n.* (KSC). Kearney Co.: Lakin *Broadhead s.n.* (MO). Meade Co.: no locality, *Hitchcock s.n.* (KSC). Ness Co.: no locality, *Hitchcock s.n.* (KSC). Pawnee Co.: no locality, *Hitchcock s.n.* (KSC). Rush Co.: no locality, *Hitchcock s.n.* (KSC). Stanton Co., no locality, *Hitchcock s.n.* (KSC). Trago Co.: no locality, *Hitchcock s.n.* (KSC). Wallace Co.: Fort Wallace, *Parry* 4 (MO); 0.5 mile s. of Sharon Springs, *Ownbey & Ownbey* 1674 (COLO, K, KSC, MICH, MIN, NEW MEX, OKL, RM, SMU).

NEW MEXICO

Chaves Co.: 3.5 miles n. of Dunken, *Ownbey & Ownbey* 1748 (MIN, NEW MEX, NY, POM). Eddy Co.: 21.8 miles n.w. of Carlsbad, *Ownbey & Ownbey* 1739 (BM, COLO, F, GH, MIN, NEW MEX, RM, SMU, UC, US); 4.9 miles w. of Hope, *Ownbey & Ownbey* 1747, *in part* (ARIZ, CAS, GH MICH, MIN, NEW MEX, OKL, US). Lincoln Co.: Gray, alt. 6000-6500 ft., *Earle & Earle* 179 (MIN, MO, NY, POM, RM, US); 0.6 mile s.w. of Capitan (formerly Gray), *Ownbey & Ownbey* 1477 (ARIZ, BM, COLO, F, MIN, NEW MEX); Gray, alt. nearly 6000 ft., *Skehan* 79 (US, lectotype of *A. squarrosa* Greene; isotypes, GH, MIN, MO, ND, NY, POM, RM, UC). Quay Co.: 2 miles w. of Tucumcari, alt. 4200 ft., *Castetter* 1214 (NEW MEX). Union Co.: 4.8 miles w. of Clayton (Hwy. 64 or 87), *Ownbey & Ownbey* 1661 (F, GH, MIN, NEW MEX, NY, RM, UC, US); 25.5 miles n.e. of Clayton (1.2 miles e. of Moses, Hwy. 18), *Ownbey & Ownbey* 1736 (COLO, ILL, K, MICH, MIN, NEW MEX, POM, TEX, WS).

OKLAHOMA

Cimarron Co.: 8.2 miles n. of Boise City, *Ownbey & Ownbey* 1659 (COLO, GH, MIN, NEW MEX, NY, OKL, RM, SMU, UC, US); Cimarron River crossing, 35.2 miles s. of Pritchett, Colo., *Ownbey & Ownbey* 1731 (ARIZ, BM, BRY, CAS, COLO, KSC, MIN, OKL). Texas Co.: 20.6 miles west of Guymon on road to Boise City, *Ownbey & Ownbey* 1658 (GH, MIN, OKL).

STATE UNCERTAIN

On prairies, upper spring of Cimarron, *Fendler* 16, in part (MO); no locality, Fremont's expedition to California, *Fremont* 470 or *s.n.*, *in part* (GH, US); on the Arkansas, Santa Fe road, *Wislizenus* 432 (MO).

8b. ARGEMONE SQUARROSA Greene subsp. **glabrata** G. B. Ownb., subsp. nov.

A. platyceras Fedde, in Pflanzenr. 4 (104): 283. 1909, in small part; not A. *platyceras* L. & O.

Herba perennis latice flavo. Caules 1-plures, 4-6 dm. alti, moderate vel copiose aculeati, aculeis tenuibus magnitudine regulari. Folia profunde vel repande lobata, superioribus manifeste caulem aplectentibus, subter in venis principalibus sparsissime aculeata, supra inermia vel sparsissime aculeata. Capsulae 4-5-carpellatae robuste spinescentes, spinis maximis 8-12 mm. longis, atque paucis vel multis et parvioribus spinis et aculeis interspersis. Semina usque ad 2.5 mm. longa.

Perennial with yellow latex; stems 1-several from the base, 4-6 dm. tall, widely branched in the upper portion, the branches stout, the stems at maturity more or less flat-topped, moderately to copiously prickly with slender, rather even-sized, perpendicular prickles; leaves distinctly bluish, deeply lobed below, the segments oblong, less deeply to shallowly lobed upward, the uppermost leaves distinctly clasping the stem, the margins with acute points or secondary lobes, each of which is terminated by a rigid prickle, the leaf surfaces sparingly prickly on the main veins beneath, smooth or very sparingly prickly on the main veins above, the areas between the larger veins essentially smooth both above and below; buds subspherical, the body 16-18 mm. broad, 16-20 mm. long, sparingly prickly, the sepal horns more or less angular in cross-section, 8-11 mm. long, very sparsely prickly, terminated by a rigid spine; flowers closely subtended by 1-2 reduced leaves, 8-11 cm. in diameter; petals white; stamens numerons, 150 or more, the filaments pale yellow, the anthers yellow; stigma purple, 3-4 mm. broad, 2-3 mm. high, 4-5 lobed; capsules 4-5-carpellate, oblong-elliptic to lance-ovate, the width, exclusive of armature, 14-18 mm., the length, including the stigma, 25-50 mm., armed with stout, scattered, basally herbaceous, spreading or reflexed spines, the largest spines usually 8-12 mm. long and provided with a few secondary prickles, terminated by a stont, indurated point, the capsules also provided with few to numerous very uneven-sized, smaller spines and prickles; seeds to 2.5 mm. long. (Ill.: Fig. 8, 4; Dist.: Fig. 13.)

Holotype: *Gerald B. Ownbey & Findley Ownbey* 1745, from 11.5 miles northeast of Pine Springs, Culberson Co., Texas, Aug. 11, 1953 (MIN; isotypes, GH, NY, SMU, US).

Habitat and distribution: Arid slopes and valleys, western Texas and southeastern New Mexico, at altitudes of about 2000-5000 ft.

Flowering and fruiting dates: First flowers appear in late April or early May and flowering continues as conditions permit through the summer; fruits mature from mid-June through August.

A. squarrosa subsp. *glabrata* differs from subsp. *squarrosa* principally in the amounts of surface enations present. Most of the finer prickles on the stem, buds and fruits of subsp. *squarrosa* are absent in subsp. *glabrata*. In the latter subspecies, the leaves are only sparingly prickly on the veins below, prickles are usually totally lacking on the veins above and the areas between the larger veins above and below are essentially smooth. However, occasional plants of subsp. *squarrosa* with less than the usual amount of surface enations sometimes are found in western Kansas and southeastern Colorado.

Collectors regularly have identified specimens of *A. squarrosa* subsp. *glabarata* as *A. platyceras* L. & O., with rare exceptions. Its affinity with *A. squarrosa* Greene has not been recognized previously. The relationship which this subspecies bears to the other white-flowered species found in

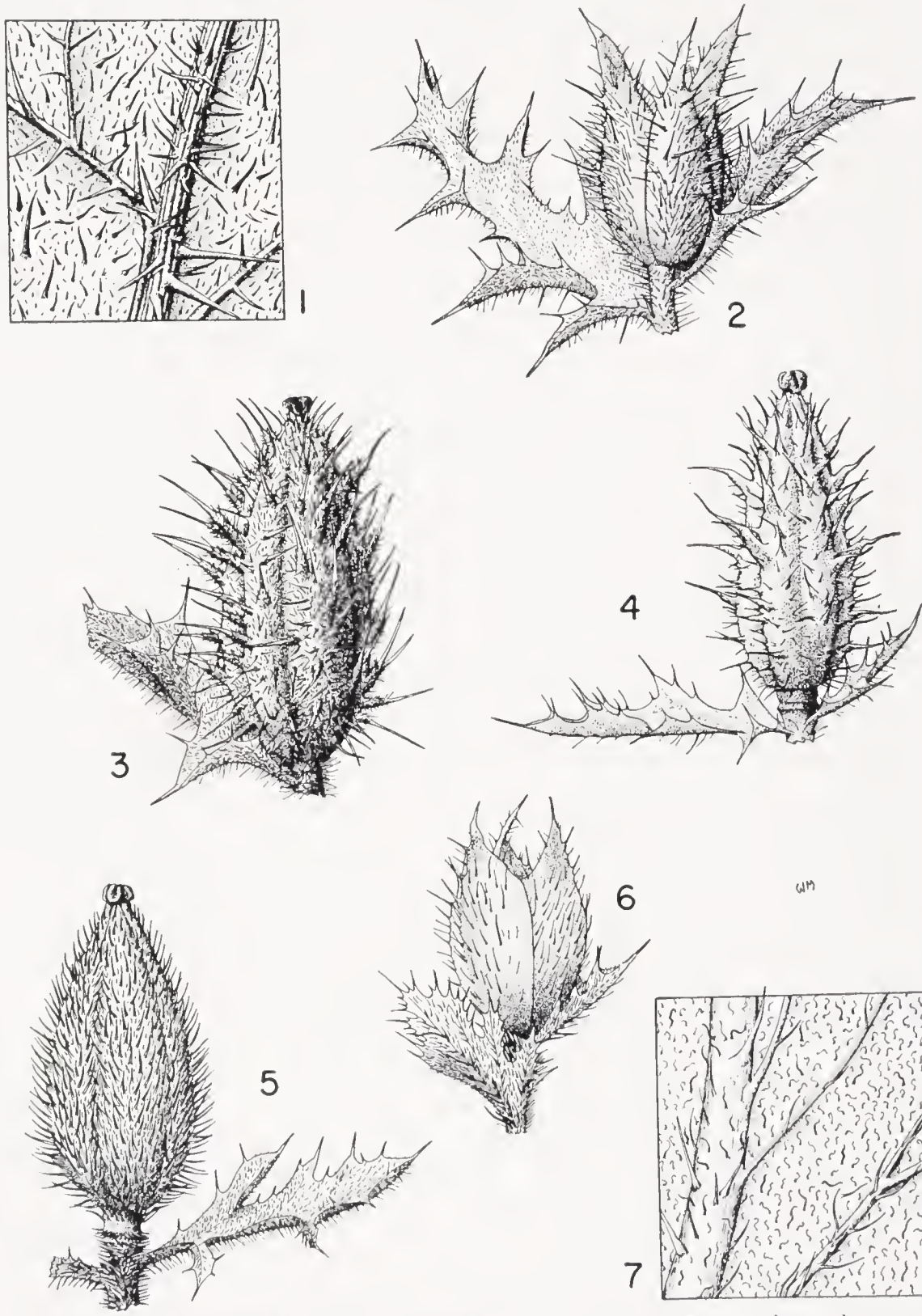

FIG. 8. 1-3. *A. squarrosa* subsp. *squarrosa*. 1. Leaf, under surface along midrib × 4. From authentic material. 2. Bud × 1. Liquid preserved material of *Ownbey & Ownbey* 1659 (MIN). 3. Capsule × 1. Liquid preserved material of *Ownbey & Ownbey* 1705 (MIN). 4. *A. squarrosa* subsp. *glabrata*. Capsule × 1. Liquid preserved material from type collection, *Ownbey & Ownbey* 1745 (MIN). 5-7. *A. hispida*. 5. Capsule × 1. Liquid preserved material of *Ownbey & Ownbey* 1697 (MIN). 6. Bud × 1. Liquid preserved material of *Ownbey & Ownbey* 1663 (MIN). 7. Leaf, under surface along midrib × 4. From authentic material.

west Texas and adjacent Mexico such as *A. chisosensis* and *A. sanguinea* needs clarification, but may well be close. No cytological or genetical evidence bearing on the question is available at present.

The geographical distribution of *A. squarrosa* subsp. *glabrata* is natural, with the exception of the records from Tom Green Co., Texas. These records possibly may represent introductions.

Specimens examined: UNITED STATES.

New Mexico

Eddy Co.: Black River, dry field, *Standley* 40467 (US); Hope, *Campbell s.n.* (CAS); sandy ridges, Carlsbad Caverns, *Conris* 84 (RM); 4.9 miles w. of Hope, *Ownbey & Ownbey* 1747, *in part* (GH, MIN, NEW MEX).

Texas

Brewster Co.: near Alpine, *Hinckley* 578 or *s.n.* (F, NY, TEX). Culberson Co.: 1 mile s. of Pine Springs, *Ownbey & Ownbey* 1741 (ARIZ, CAS, COLO, F, MIN); 11.5 miles n.e. of Pine Springs, *Ownbey & Ownbey* 1745 (MIN, holotype of *A. squarrosa* subsp. *glabrata* Ownb.; isotypes, GH, NY, SMU, US). Dickens Co.: 4.5 miles n.e. of Spur, *Cory* 13593 (GH). Jeff Davis Co.: Fern Canyon, Davis Mts., *Cory* 9423 (GH). Presidio Co.: w. of Marfa, *Whitehouse* 11815 (SMU). Tom Green Co.: San Angelo, *Reverchon* 3707 (MO); Knickerbocker Ranch, Dove Creek, *Tweedy* 144 (US).

9. Argemone hispida Gray, Pl. Fend., in Mem. Am. Acad. 4: 5. 1849, excluding description of fruits.

A. hispida Walp., Ann. 2: 25. 1852; Hemsl., Biol. Cent. Am., Bot. 1: 27. 1879, as to original citation only; Hemsl., l.c., 4: 4. 1886; Prantl & Kündig, in Engl. & Prantl, Nat. Pflanzenf. 3 (2): 141. 1889; Brit., Man., p. 439. 1901, in part; Small, Fl. s.e. U. S., p. 462. 1903, as to New Mexico distribution; Rydb., Fl. Colo., p. 149. 1906, excluding Utah distribution; Britton & Brown, Ill. Fl., ed. 2, 2: 139. 1913, as to Wyoming to New Mexico distribution only; Woot. & Standl., Fl. N. Mex., in Contr. U. S. Nat. Herb. 19: 261. 1915, as to New Mexico distribution; Rydb., Fl. R. Mts., p. 318. 1917, in part; Rydb., Fl. Pr. & Pl., p. 353. 1932, excluding Kansas and Utah distributions.

A. mexicana Porter, in Hayden, Rep. Geol. Surv. 1870: 473. 1871; Port. & Coult., Syn. Fl. Colo., p. 6. 1874, in part; Prantl & Kündig, in Engl. & Prantl, Nat Pflanzenf. 3 (2): 135, fig. 83B. 1889; not *A. mexicana* L.

A. mexicana var. *hispida* Torr., in Rothrock, Reports, p. 61. 1878, excluding Utah collections; not *A. mexicana* L.

A. platyceras Coult., Man., p. 13. 1885, in part; Coult., in Contr. U. S. Nat. Herb. 2: 12. 1891, as to synonym *A. hispida;* Gray, Syn. Fl. N. Am. 1 (1): 88. 1895, in part; Weber, Hand. Pl. Colo. Fr. R., p. 106. 1953; not *A. platyceras* L. & O.

A. mexicana β *albiflora* var. *hispida* Kuntze, Rev. Gen. 1: 12. 1891, as to Wyoming distribution; not *A. mexicana* L.; not *A. albiflora* Hornem.

A. platyceras var. *hispida* Prain, in Journ. Bot. 33: 367. 1895, mainly; Eastwood, Erythea 4: 96. 1896, as to Colorado distribution; Fedde, in Pflanzenr. 4 (104): 285, in large part, 274, fig. 36P, R. 1909; Abrams, Ill. Fl., 2: 231. 1944, as to New Mexico distribution; Harringt., Man. Pl. Colo., p. 253. 1954, excluding synonym *A. squarrosa.*

A. bipinnatifida Greene, in Pittonia 3: 346. 1898.

Enomegra hispida Nels., Analyt. Key Fl. Pl. Rocky Mt. Reg., p. 27. 1902; Nels., in Bot. Gaz. 34: 366. 1902; Nels., Coult. & Nels., New Man. Bot., p. 205. 1909.

Enomegra bipinnatifida Nels., in Bot. Gaz. 34: 366. 1902.

Argemone platyceras var. *hispida* subvar. *bipinnatifida* Fedde, in Pflanzenr. 4 (104): 286. 1909; not *A. platyceras* L. & O.

Perennial, the latex white with a faint yellow cast; stems often several to many from the base, usually 3-6 dm. tall, sparingly branched towards the top, the later branches overtopping the main axis, densely prickly throughout with prickles of various sizes, and also more or less densely hispid with crisped indumentum (upon drying); leaves bluish, the upper ones sometimes shallowly lobed, the lower ones usually deeply lobed to four-fifths or more of the distance to the midrib, the lobes approximately oblong and with secondary, deltoid lobes or points, each of which is terminated by a weak prickle, the leaves often rather densely prickly on the midrib below, rather weakly prickly to unarmed on the secondary veins below and the veins above, both surfaces of the leaves also sparsely to densely minutely crisped-hispid; buds usually rather closely subtended by the foliar bracts, oblong, the body 14-18 mm. broad, 16-20 mm. long, sparsely to copiously prickly as well as hispid, the sepal horns 4-7 mm. long, usually prominently prickly, terminated by a flattened, indurated spine; flowers 7-10 cm. in diameter when fully expanded; petals white, discoloring upon drying; stamens numerous, 150 or more, the filaments pale yellow, the anthers yellow; stigma 3-4-lobed; capsules 3-4 carpellate, ovate, the width, not including the armature, 12-18 mm., the length, including the stigma, 30-40 (-50) mm., densely prickly with straight or incurved prickles, the largest of which rarely exceeds 5 mm. in length, also more or less crisped-hispid, the armature completely or nearly obscuring the surface; seeds about 2.5 mm. long. (Ill.: Fig. 8, 5-7; Dist.: Fig. 13.)

Lectotype: *Fendler* 16, *in part,* from low, sandy places around Santa Fe, New Mexico, June and July, 1847 (GH; isotypes, F, GH, MO, NY, PH, UC, US). The number *16* is that given by Gray to Fendler's collections assigned to the species. The lectotype and isotypes are of flowering material only.

Habitat and distribution: Flat prairies, slopes, and alluvial valley floors, in sandy or clay soils, foothills of the Rocky Mountains from southeastern Wyoming south through Colorado to central New Mexico at altitudes of usually 5500-7500 ft.

Flowering and fruiting dates: Flowers open from about June 1 through the summer to about Sept. 15; fruits are matured from about Aug. 1 to Sept. 20. Plants usually do not have both flowers and mature fruits simultaneously.

A. hispida is well defined morphologically and geographically. Its morphological definition rests largely upon the presence in greater or lesser density of crisped-hispid indumentum on the stem and leaves, in addition to the abundant though comparatively weak prickles of the stem. It seems to be closely related to several other species of the southwest and Mexico. It differs from *A. squarrosa* in its smaller stature and smaller, unbranched capsular spines; it differs from *A. pleiacantha* and *A. platyceras* in the presence of the indumentum described above and in size and shape of the sepal horns; it differs from *A. munita* in the fact that the surface armature of *A. munita*, when present, consists of minute prickles which are not crisped. Its geographical distribution is sympatric with no other closely related species. Much of its range is, however, also common to *A. polyanthemus* to which it probably bears no close relationship. I have observed

these two species growing together north of Ft. Collins, Colorado, and at this locality there was no evidence of natural hybridization. Probably they are completely incompatible.

The original description of *A. hispida* was based upon specimens of two species, true *A. hispida* and *A. squarrosa*, both collected by Fendler and assigned the same number, 16, by Gray. The type collection of *A. hispida*, from Santa Fe, comprised a large series of plants in bud and flower. The single specimen seen of *A. squarrosa* used in drawing up the original description of *A. hispida* came from the vicinity of the "Upper spring of Cimaron," and is in fruit. As a result of this initial confusion the original description of *A. hispida* applies in part to two species; the description of fruits applies strictly to *A. squarrosa*. When Greene described *A. squarrosa* he inadvertently supplied a name for the anomalous element in *A. hispida*. The two species are, however, persistently confused even to the present day.

The original confusion in *A. hispida* has been further compounded by later botanists by the identification of specimens of still other species as *A. hispida*. Further, the complex of species passing as *A. hispida* has often been completely merged with *A. platyceras* Link & Otto, as was done by Gray himself in his Synoptical Flora, or has been given varietal status under *A. platyceras*, as was done by Prain.

Various persons have attempted to resolve some of the difficulties ereted by the excessive consolidation of biologically diverse elements described above by describing these anomalous elements as new species. This procedure has proved to be sound. The first such segregate species described was *A. munita* Dur. & Hilg. from southern California, described in 1855. This was followed by *A. bipinnatifida* Greene (1898), *A. squarrosa* Greene (1899), *A. sanguinea* Greene (1899), *A. rotundata* Rydberg (1902), *A. pleiacantha* Greene (1908), *A. aurantiaca* Ownbey and *A. echinata* Ownbey in the present paper. Of these, *A. bipinnatifida* alone falls directly into synonomy under *A. hispida*, in the restricted sense. I have not found sufficient basis to justify recognition of this proposed taxon at any rank. All of the species listed above which were described before 1909, with the exception of *A. squarrosa* which was allowed to stand, were reduced to varietal or subvarietal status or to synonomy under *A. platyceras* by Fedde in his monograph of *Argemone*. *A. hispida* was retained as a variety, but specimens cited under it mostly belong with one or another of the other subordinate groups recognized. Other taxa besides those mentioned above were also included in *A. platyceras* by Fedde.

A. platyceras var. *hispida* of Prain's monograph, judging from the specimens cited, consisted mainly of *A. hispida* Gray. Also cited, however, were specimens of *A. munita* subspp. *munita* and *rotundata*. Despite

Prain's arguments indicating that Durand himself ultimately decided that his *A. munita* was really synonymous with *A. hispida* Gray, both authors were undoubtedly mistaken on this point.

In Fedde's revision, *A. platyceras* var. *hispida*, as to cited specimens, consisted largely of *A. hispida* and largely of *A. munita* subsp. *rotundata*, and to a small extent of *A. munita* subsp. *munita* and *A. echinata*.

The genus *Enomegra* erected by Nelson on the basis of latex color to include *Argemone hispida* and its synonym *A. bipinnatifida* does not merit recognition. The latex is not actually white in *A. hispida* as is affirmed by Nelson, but has a faint yellow cast. Other species of *Argemone* also have whitish latex in whole or in part, for example, *A. gracilenta*, *A. munita* and *A. pleiacantha*.

Specimens examined: UNITED STATES.

Colorado

Arapahoe Co.: Military Park, *Smith s.n.* (MO). Boulder Co.: near Boulder, alt. 5000-6000 ft., *Tweedy* 4965 (NY, RM). Chaffee Co.: Buena Vista, *Applegate* 8534 (DS). Costilla Co.: Veta Pass, alt. 2400-2700 m., *Rydberg & Vreeland* 6261 (NY, RM). Denver Co.: Barnum (Junction), *Eastwood* 119 (CAS, F, GH, MO, UC, US); along the Platte River, Denver, *Jones* 218 (MO, NY, POM, US). El Paso Co.: Colorado City, *Bacigalupi* 704 (DS, GH, UC); Colorado Springs, *Eastwood s.n.* (MIN); Manitou, *Woodward s.n.* (GH). Fremont Co.: near Canyon City, *Brandegee* 108 (MO, PH, UC). Huerfano Co.: 26.8 miles n.w. of Walsenburg, Hwy. 85, *Ownbey & Ownbey* 1487 (MIN); Huerfano Valley near Gardner, alt. 7000 ft., *Vreeland* 650 (NY, RM). Jefferson Co.: west of Wheatridge, *Bethel s.n.* (CAS); near Mt. Morrison s.w. of Denver, alt. 6000 ft., *Constance & Rollins* 1914 (UC). Larimer Co.: near Ft. Collins, *Crandall* 3 (GH); foothills, along Buckhorn Creek, *Osterhout s.n.* (MIN, RM, UC); about 25 miles n. of Ft. Collins, *Ownbey & Ownbey* 1310 (CAS, MIN, NY, UC). Las Animas Co.: 5.3 miles n.e. of Trinidad on road to La Junta, *Ownbey & Ownbey* 1663 (ARIZ, COLO, GH, MICH, MIN, NEW MEX, POM, RM, US, UTC). Otero Co.: 32.9 miles s.e. of La Junta between Bloom and Delhi, on road to Trinidad, *Ownbey & Ownbey* 1666 (COLO, GH, K, MIN, RM, UTC). Pueblo Co.: Pueblo, *Woodward s.n.* (GH). Weld Co.: New Windsor, *Osterhout* 2319 (NY, RM). County unknown: lat. 39°-41°, *Hall & Harbour s.n.* (GH).

New Mexico

Colfax Co.: about 10 miles e. of Raton, alt. 6500 ft., *Robbins* 583 (UC); vicinity of Raton, *Rose & Fiteh* 17560 (US). Mora Co.: 1.9 miles s.w. of Wagon Mound, *Ownbey & Ownbey* 1484 (COLO, MIN, NEW MEX, OKL, UTC). San Miguel Co.: Canyon Bonito, Las Vegas, alt. 2300 m., *Arsé* 19222 (F). Santa Fe Co.: near Santa Fe, *Fendler* 16, *in part* (GH, lectotype of *A. hispida* Gray; isotypes, F, GH, MO, NY, PH, UC, US); Santa Fe, alt. 7200 ft., *Heller & Heller* 3704 (DS, GH, KANU, KSC, MIN, MO, ND, NY, US); Santa Fe, *Rusby* 20 (TEX, US). Taos Co.: near Gusdorf, *O'Byrne & Magner* 3417-4 (MO). Union Co.: 1.4 miles w. of Des Moines, *Ownbey & Ownbey* 1662 (MIN); near the Sierra Grande, alt. 2100-2925 m., *Standley* 6052 (US).

Wyoming

Albany Co.: Sybille (i.e., Sibylee) Hills, *Nelson* 314 (ND, holotype of A. bipinnatifida Greene; isotypes, GH, MIN, MO, RM, US); Chug (i.e., Chugwater) Creek, *Nelson* 7344 (GH, MIN, MO, NY, POM, RM, US); 34.6 miles s.w. of Wheatland, Hwy. 34,

Ownbey & Ownbey 1500 (ARIZ, COLO, KSC, MIN, SMU); Sherman Hill, alt. 8000 ft., *Williams* 1059 (CAS, GH, MO, NY, RM). Laramie Co.: Cheyenne *Overton* 105X (RM). Platte Co.: Chugwater station, *Buffum* 46 (RM); Wheatland, *Nelson* 286 (NY).

State Uncertain

Fremont's expedition to California, *Fremont* 8 (GH).

10. Argemone munita Dur. & Hilg., in Journ. Acad. Nat. Sci. Phila., series 2, 3: 37. 1854; Dur. & Hilg., in Pac. R. Rep. 5 (3): 5, t. 1. 1855.

Annual or perennial with pale lemon-yellow, rarely more intensely yellow latex; stems 1-10 (-25), 4-16 dm. tall, often purplish (except in subsp. *argentea*), sparingly to copiously branched, sparingly prickly (in subsp. *robusta*) to moderately prickly (in subsp. *munita*) to rather closely or densely prickly (in subspp. *rotundata* & *argentea*); leaves oblanceolate below, progressively elliptical to ovate or lanceolate upward, the uppermost usually partially clasping the stem; lower leaves lobed to about one-half the distance to the midrib or less, the lobes usually manifestly rounded at the apex, sometimes angular, the middle and upper leaves usually more shallowly lobed or the margins sharply angular; leaf margins armed with prickles, less closely so in subspp. *robusta* and *munita*, more closely so in subspp. *rotundata* and *argentea*; leaf surfaces very sparingly prickly only on the main veins (mostly beneath, in subsp. *robusta*), sparingly prickly on the veins and intervein surfaces (in subsp. *munita*), more copiously prickly on the veins and intervein surfaces (in subsp. *argentea*) to often densely prickly (in subsp. *rotundata*); buds oblong, elliptic-oblong or oblong-obovate, the body 10-16 mm. broad, 12-22 mm. long, prickly with perpendicular prickles, sparingly so (in subspp. *robusta* and *munita*) to copiously prickly with simple prickles (in subsp. *argentea*) or copiously prickly with the larger prickles sometimes compound (in subsp. *rotundata*), the sepal horns usually terete, or sometimes somewhat flattened or angular in cross-section, 6-8 (4-10) mm. long, smooth to densely prickly, the apical spine often enlarged and flattened at its juncture with the vegetative basal portion of the horn (especially in subsp. *rotundata*); flowers 5-10 (-13) cm. in diameter when fully expanded, the nearest subtending foliar bract often separated by several mm. from the base of the flower; petals white, obcuneate to obovate; stamens numerous, about 150-250 or more, the filaments pale yellow, the anthers yellow; stigma purple, 3-5 lobed, about 2-4 mm. wide, 2.0-3.5 mm. high; style evident, usually less than 2 mm. long in fruit; capsules 3-5-carpellate, at maturity ovate, elliptical, elliptic-lanceolate or lanceolate, the width, excluding the armature, 9-15 (-18) mm., the length, including the stigma and style, 35-55 mm., armed with mostly large, widely spaced spines (in subsp. *robusta*), these interspersed with a few lesser spines and prickles (in subsp. *munita*) or interspersed with numerous lesser spines and prickles (especially in subsp. *rotundata*, less so in subsp. *argentea*), the longest spines seldom exceeding 8 mm. in length, the capsular surface clearly visible through the armature (in subsp. *robusta*) to much obscured (in subsp. *rotundata*); seeds 1.8-2.2 (-2.6) mm. long.

Lectotype: *A. L. Heermann, s.n.*, from Williamson's Pass,[1] Los Angeles

[1] The exact location of Williamson's Pass is given by W. P. Blake in Pac. R. R. Rept. 5 (2): 67. 1857 (i.e., Williamson's Report), as follows: "The position of this pass, and its direction, will be seen upon the general map and on the geological map of Tejon and vicinity, Map II, Chapter XV. The pass extends from the Great Basin to the Rancho of San Francisquito, which is in one of the valleys of the Pacific slope. Its entrance on the Great Basin is near the meridian 118° and latitude 34° 30′, and its direction a little south of west; the distance through the mountains from the Great Basin side to the open valley of the Santa Clara river is about 20 miles. The altitude of the summit level is 3,164 feet above the sea." The maps mentioned by Blake are, first, "General Map of Explorations and Surveys in California" to be found in Vol. 11 of the Reports. The pass in question is termed New Pass on this map, but the elevation and

Co., California, date not given (PH; isotype, P, not seen, Durand Herbarium, according to Prain, 1895, p. 368).

Habitat and distribution: Deserts, foothills, and mountain slopes to middle elevations, northern Baja California to northern California, northwestern New Mexico, Nevada and Utah.

Flowering and fruiting dates: See under the subspecies.

A specimen of *Argemone* collected by Dr. A. L. Heermann at Williamson's Pass, California, is on deposit at the Philadelphia Academy. It is undoubtedly part of the original collection of the species, and in my opinion should be designated the lectotype. The lectotype consists of two fragments of branches, each with one flower. The stems are rather coarsely and evenly prickly with scattered prickles of about 3-6 mm. in length, and are otherwise glabrous. Portions of four leaves are present. These are marginally prickly and with a few lesser prickles on the veins of both surfaces and are otherwise glabrous. One bud is present; it is subspherical, the body about 14 mm. broad and 17 mm. long, the sepal horns about 9 mm. long. The sepals are sparsely prickly, mostly distally and on the un-indurated basal portion of the horns, with prickles about 3 mm. long standing about perpendicular to the surface. The flowers are white and about 9 cm. in diameter. The young fruits are evenly long-prickly with straight prickles which presumably would be quite widely scattered over the capsular surface at maturity.

Dr. Prain (1895) under *A. platyceras* var. *hispida* cites a fragment of *Argemone* collected at Williamson's Pass in California by Heermann and deposited in Durand's herbarium at Paris. Despite Prain's arguments that Durand himself ultimately decided that his species, as represented by this Paris specimen, was synonymous with *A. hispida* Gray, there is no doubt that both Prain and Durand were mistaken on this point.

Since the Heermann fragment at Paris is stated by Prain to be hispid, I cannot avoid the thought that this specimen, which I have not seen, may well represent an intermediate between subsp. *munita* and subsp. *rotundata*. The same holds true to some extent for the lectotype, although its surface armature is very much in the direction of the taxon I am designating as subsp. *munita*. The original illustration of *A. munita* shows a plant with far more prickly stems than I would consider typical for subsp. *munita* as herein circumscribed.

The determination of the lectotype of this species as possibly inter-

location are correct for Williamson's Pass and they doubtless are the same. The other map mentioned by Blake is a part of his own paper in Vol. 5 of the Reports, facing p. 196. Here the pass is designated Williamson's Pass. The latitude and longtitude given by Blake can be located on detailed topographic maps of the present day. The town of Vincent at Long. 118° 7′ and Lat. 34° 30′ and an altitude of 3210 feet lies within the pass. The type locality of *A. munita* Dur. & Hilg. is in this vicinity.

mediate between two included subspecies, viz. subspp. *munita* and *rotundata*, creates certain difficulties concerning which subspecies should include the lectotype. I can find nothing in the International Rules covering this situation. In the present instance I am arbitrarily classifying the lectotype with the more glabrous subspecies which it more closely resembles. It automatically becomes the type of this subspecies as well as that of the species in the broad sense. This has added advantages, since subsp. *rotundata* already has a type, that of *A. rotundata* Rydb. No new names are needed and only one new combination is required if this procedure is adopted.

A. munita subspp. *robusta* and *rotundata* represent the morphological extremes of the species. They are connected through subsp. *munita* by transitional forms. Subsp. *argentea* is a component of the species which occupies a position outside the above series. Its closest presumed affinities are with subsp. *rotundata*.

Since *A. munita* is a highly variable species including plants ranging from densely hispid to nearly smooth, its precise definition is difficult. The tendency towards rather short and broad, apically rounded, leaf lobes is evident in each subspecies. The indurated apical spine of the sepal horn tends to be flattened and enlarged at its juncture with the vegetative lower part of the horn, especially in subsp. *rotundata*. Subspp. *argentea* and *rotundata* are perennials, subsp. *munita* annual or perennial, and subsp. *robusta* annual. Were it not for the intergrading forms between subspp. *munita* and *rotundata*, I would be inclined to separate *A. munita* into two species, *A. munita*, in the strict sense, composed of two subspecies, *munita* and *robusta*, and *A. rotundata*, composed of two subspecies, *rotundata* and *argentea*. It is known from my own work that the haploid number of chromosomes in *A. munita*, all four subspecies, is 14. This in itself, however, provides no evidence for or against treating the complex as a single species or as two species. No experimental crosses among the four subspecies have been attempted.

In literature, *A. platyceras* L. & O., in the broad sense, has usually included, among other diverse elements, the three taxa which I designate as *A. munita* subsp. *munita*, *A. munita* subsp. *robusta*, and *A. munita* subsp. *argentea*. *A. platyceras* var. *hispida* (Gray) Prain, in literature, includes true *A. hispida* Gray combined, in most cases, with *A. munita* subsp. *rotundata*. When American authors have accorded *A. hispida* Gray specific rank it has been in the above sense, i.e., with the inclusion of *A. munita* subsp. *rotundata*. These viewpoints can no longer be sustained. For further discussion see the treatments of *A. hispida* and *A. platyceras* in this paper.

In his study of California *Argemone* species, Carl B. Wolf (1938) made an excellent disposition of the California specimens of *A. munita* available to him. All specimens were placed, with misgivings, under the traditional names *A. platyceras* L. & O. and *A. platyceras* var. *hispida* (Gray) Prain. Many speeimens were elassified as intermediate between the two. My circumscription of *A. munita* subsp. *munita* is equivalent to Wolf's *A. platyceras* exeept that I have restricted the taxon to the less prickly forms and have removed entirely specimens of two new subspecies, viz., subsp. *argentea* and subsp. *robusta*, with a consequent contraction of the distributional range. My circumscription of *A. munita* subsp. *rotundata* is equivalent to Wolf's *A. platyceras* var. *hispida* except that I have allowed for slightly more variation in this taxon than did Wolf. Intermediacy of numerous speeimens between subspp. *munita* and *rotundata* was recognized by Wolf, and in most instances where specimens were so annotated by Wolf I concur fully with his viewpoint.

A marked relationship between fire and germination of the seeds of *A. munita* is evident. *A. munita* subsp. *robusta* was abundant in a reeently burned area and nowhere else, at the type locality in Orange Co., Calif., when the writer visited the site in 1954. A large population of plants determined as intermediates between subspp. *munita* and *rotundata* were seen on another burn located 7 miles west of Ravenna, Los Angeles Co., Calif., by the writer, also in 1954. A very vigorous population of about 200 individuals, all of the current season, of *A. munita* subsp. *munita*, was seen on a new burn situated 1.6 miles s.w. of Emory store, just east of Palomar Mt., San Diego Co., Calif., by the writer, again in 1954. Good germination of the seeds of the last subspecies was obtained by personnel of the Raneho Santa Ana Botanic Garden when vegetable material was burned on the surface of the flats just after planting of the seeds. The increased germination of the seeds of many western plants obtained by heat treatments is well known.

Key to the subspecies of *A. munita:*

1. Stems rather sparingly to moderately prickly, i.e., with usually 0-80 prickles per sq. cm. on the stem about 5 cm. below the base of the capsule which terminates the primary axis; buds very sparingly to moderately prickly; leaf surfaces smooth or sparingly prickly on the veins and intervein surfaces; capsules distantly to more closely spinescent, the surface clearly visible.

2. Stems very sparingly prickly, i.e., with usually 0-10 prickles per sq. cm. on the stem about 5 cm. below the base of the capsule which terminates the primary axis; buds very sparingly prickly; leaf surfaces usually totally smooth above, sparingly prickly only on the main veins beneath; capsular armature consisting almost wholly of large, widely spaced spines; Orange Co., California . . . . . 10a. *A. munita* subsp. *robusta*

2. Stems and buds more copiously prickly; leaves somewhat prickly on the veins of

both surfaces and usually also between the veins; capsular armature consisting of large spines interspersed with uneven-sized smaller ones.

3. Stems with about 10-30 prickles per sq. cm. about 5 cm. below the base of the capsule which terminates the primary axis; leaf surfaces sparingly to moderately prickly on the veins and usually on the intervein surfaces; coast ranges, northern Baja California and southern California ..... 10b. *A. munita* subsp. *munita*

3. Stems with about 50-80 prickles per sq. cm. about 5 cm. below the base of the capsule which terminates the primary axis; leaf surfaces moderately to rather copiously prickly, but not densely so on the veins and intervein surfaces; primarily in the coast ranges of California ..... 10d. Intermediates between subspp. *munita* and *rotundata*

1. Stems more closely prickly, i.e., with usually 80-500 prickles per sq. cm. on the stem about 5 cm. below the base of the capsule which terminates the primary axis; buds usually closely prickly; leaf surfaces moderately to closely prickly on the veins and intervein surfaces; capsules usually copiously armed with large spines interspersed with smaller, uneven-sized spines and prickles, the surface partially obscured.

4. Stems glaucous, when alive usually with purplish coloration, usually closely armed with uneven-sized, perpendicular prickles of moderate length; buds usually closely beset with large, often compound, perpendicular prickles interspersed with smaller, uneven-sized simple ones.

5. Stems with about 80-180 prickles per sq. cm. about 5 cm. below the base of the capsule which terminates the primary axis; prickles of the buds always simple; generally less copiously prickly throughout than subsp. *rotundata;* primarily in the coast ranges of California ..... 10d. Intermediates between subspp. *munita* and *rotundata*

5. Stems usually with about 120-500 prickles per sq. cm. about 5 cm. below the base of the capsule which terminates the primary axis; largest prickles of buds sometimes compound; mainly on the eastern slopes of the Sierra Nevada, California, to Utah ..... 10c. *A. munita* subsp. *rotundata*

4. Stems glaucous, greenish-white when alive, lacking purplish coloration, usually closely armed with very long, uneven-sized, perpendicular prickles, i.e., with about 100-300 prickles per sq. cm. about 5 cm. below the base of the capsule which terminates the primary axis; buds usually closely beset with simple, slender, more equal-sized ascending prickles; desert ranges of southern California, Death Valley, adjacent Arizona and southern Nevada ..... 10c. *A. munita* subsp. *argentea*

10a. Argemone munita Dur. & Hilg. subsp. robusta G. B. Ownb., subsp. nov.

A. platyceras Munz, Man. S. Calif. Bot., p. 182. 1935, in small part; Wolf, in Rancho Santa Ana Bot. Gard. Occ. Papers, ser. 1 (2): 60. 1938, in small part; not *A. platyceras* L. & O.

Herba annua latice citreo-flavo. Caules 5-16 dm. alti, sparse aculeati. Folia glauca, foliis terminalibus amplexicaulibus, subter sparsissime aculeata in venis, supra inermia. Alabastra sparsissime aculeata, aculeis perpendicularibus, petalis albis; staminibus circa 250. Capsulae 3-4-carpellatae, ellipticae vel elliptico-lanceolatae spinis sparsis armatae. Semina circa 2.5 mm. longa.

Coarse annual with lemon-yellow latex; stems 1, 5-16 dm. tall, branched in the upper one-half, sparsely prickly with stout, perpendicular prickles, often tinged with purple; lower leaves to 3 dm. long, oblanceolate, not clasping, shallowly lobed; middle and upper leaves progressively smaller, lobed to about one-half the distance to the midrib, the uppermost ovate and clasping the stem; all the leaves fleshy in texture when fresh, glaucous, the margins toothed, each tooth terminated by a prickle, the lower surfaces armed with a very few prickles on the midrib and larger secondary veins, the upper surfaces usually totally smooth; buds slightly longer than broad, the width 12-16 mm., the length 14-22 mm., very sparingly prickly with perpendicular prickles, the sepal horns

slender, somewhat flattened, 6-8 mm. long, smooth; flowers 6-10 cm. in diameter, usually not closely subtended by the much reduced bracteate uppermost leaves; petals white, broadly obcuneate to obovate; stamens often 250 or more, the anthers yellow, the filaments lemon-yellow; stigma purple, 3-4-lobed, about 2-3 mm. wide and 2 mm. high; style evident in fruit; capsules 3-4-carpellate, elliptical to elliptic-lanceolate, the width, not including the armature, 10-18 mm., the length, including the stigma, 35-50 mm., armed with scattered, mostly subequal, often reflexed spines the largest of which are 6-8 mm. long, the capsular surface clearly visible through the armature; seeds about 2.5 mm. long. (Ill.: Fig. 10, 4-5; Dist.: Fig. 13.)

Holotype: *Carl B. Wolf* 5403, collected on the summit of Santiago Peak, Santa Ana Mts., at an elevation of 5680 feet, Orange Co., California, Aug. 24, 1933 (UC; isotypes, CAS, DS, RSA, US).

Habitat and distribution: Dry, rocky soil, arid, sunny slopes, Santa Ana Mts., Orange Co., Calif., at elevations of about 5000 to 5680 ft.

Flowering and fruiting dates: Flowers first appear about June 15 and continue to open through the summer; fruits mature from about July 15 until autumn.

This subspecies is distinguished by its stout, sparingly prickly, annual stems, its thick, fleshy leaves which are only sparingly prickly beneath and mostly totally smooth above, by the clasping upper leaves, by the large, open inflorescences, and by the capsule armature which consists almost wholly of large, widely-spaced spines.

In my opinion, *A. munita* subsp. *robusta* is suffiicently well marked to justify recognition. However, it does intergrade with subsp. *munita* and may be considered to be the smoothest aspect of a series of forms leading through subsp. *munita* to subsp. *rotundata*. The similarity of this subspecies with some populations of *A. pleiacantha* subsp. *ambigua* is very close. The relationships of these two taxa have not been sufficiently investigated.

All of the type material of subsp. *robusta* is in fruit. An ample series of plants in bud, flower and all stages of fruit was collected by my wife and myself at the type locality in 1954. The accompanying description is drawn largely from these latter specimens.

Specimens examined: UNITED STATES.

California

Orange Co.: between Modjeska Peak and Santiago Peak, alt. ca. 5000 ft., *Ownbey & Ownbey* 2177 (ARIZ, BM, BRY, CAS, COLO, DAO, F, GH, ILL, K, MEXU, MICH, MIN, MO, NEW MEX, NY, RM, RSA, SMU, TEX, UC, UTC, US, WS); summit of Santiago Peak, Santa Ana Mts., alt. 5680 ft., *Wolf* 5403 (UC, holotype of *A. munita* Dur. & Hilg. subsp. *robusta* Ownb.; isotypes, CAS, DS, RSA, US); main divide motorway between Santiago Peak and Modjeska Peak, Santa Ana Mts., alt. ca. 5400 ft., *Wolf* 9382 (CAS, DS, RSA, UC, US).

10b. Argemone munita Dur. and Hilg. subsp. munita

A. munita Dur. & Hilg., in Journ. Acad. Nat. Sci. Phila., series 2, 3: 37. 1854; Dur. & Hilg., in Pac. R. Rep. 5 (3): 5, t. 1. 1855; Mueller, in Walp., Ann. 4: 170. 1857; Mueller, l.c., 7: 85. 1868.

A. platyceras Gray, Syn. Fl. N. Am. 1 (1): 88. 1895, in part; Eastwood, in Erythea 4: 96. 1896, in large part; Hall, Bot. Surv. San Jac. Mt., p. 81. 1902; Fedde, in Pflanzenr. 4 (104): 283. 1909, in small part; Jeps., Fl. Calif. 1: 560. 1922, in part, as to California; Jeps., Man. Fl. Pl. Calif., p. 399. 1925, in part, as to California; Munz, Man. S. Calif. Bot., p. 182. 1935, in part, as to California; Wolf, in Rancho Santa Ana Bot. Gard. Occ. Papers, ser. 1 (2): 60. 1938, in large part; Abrams, Ill. Fl., 2: 231. 1944, in part; not *A. platyceras* L. & O.

A. platyceras var. *typica* Prain, in Journ. Bot. 33: 367. 1895, in part; not *A. platyceras* L. & O.

A. platyceras var. *typica* Prain "state" β Prain, l.c., p. 368, in part; not *A. platyceras* L. & O.

A. platyceras var. *hispida* Prain, l.c., p. 367, in part; Fedde, in Pflanzenr. 4 (104): 285. 1909, in part; Davids. & Moxl., Fl. S. Calif., p. 146. 1923, in part; Abrams, Fl. Los Ang., p. 162. 1904, in part; not *A. platyceras* L. & O.; not *A. hispida* Gray.

A. intermedia Fedde, in Pflanzenr. 4 (104): 281. 1909, in part; not *A. intermedia* Sweet.

Annual or perennial with pale lemon-yellow latex; stems 1-10, 6-15 dm. tall, usually purplish, sparingly to moderately prickly; basal leaves to about 3 dm. long, usually much smaller, all the leaves more or less lobed, the lobes often not manifestly rounded, sparingly prickly at the margin and on the larger veins and often also on the intervein surfaces both above and below; buds oblong-obovate, the body about 12-16 mm. wide and 16-20 (-22) mm. long, sparingly to moderately prickly with simple, perpendicular prickles, the sepal horns terete, 6-8 (-10) mm. long, with scattered prickles at the base and terminated by a spine which is slightly flattened at its juncture with the vegetative basal portion of the horn; flowers 7-10 (-13) cm. in diameter, the subtending foliar bracts often distant; petals white, obovate to obcuneate; stamens numerous, about 150 (-250); stigma purple, 3-5-lobed, about 3-4 mm. wide and high; style often evident, to 2 mm. long; capsules 3-5-carpellate, when mature, narrowly to broadly elliptical or elliptic-ovate, the width, excluding the armature, 9-12 (-14) mm., the length, including the stigma and style, 25-40 (-45) mm., moderately spinescent with spreading spines, the largest of which are 5-8 mm. long, and also commonly with a few lesser spines and prickles, the capsular surface clearly visible through the armature; seeds 2.0-2.2 mm. long. (Ill.: Fig. 9, 1-4; Dist.: Fig. 13.)

Lectotype: That of the species.

Habitat and distribution: Dry foothills and slopes, northern Baja California northward in the Coast Ranges of California to San Luis Obispo Co., frequently in granitic soils, at altitudes of about 250-6000 ft., but most commonly from 1500 to 4500 ft.

Flowering and fruiting dates: Flowering begins about April 1 at lowest elevations but not until May or June at higher elevations, and continues until July 15 or later; early fruits reach maturity by about June 1 and fruits continue to ripen through the summer and fall.

A. munita subsp. *munita* is moderately prickly throughout with erect prickles; the prickliness of the leaf surfaces is sparse; smaller prickles are usually found interspersed with the larger spines on the capsules. The leaves often have the characteristic lobing of subsp. *rotundata* and subsp. *robusta*, but in many plants the lobes are narrower and less manifestly rounded at the apex. Transition forms to both subspp. *rotundata* and *robusta* do occur, and variation from the smoothest phase in subsp. *robusta* to the most prickly phase in subsp. *rotundata* is continuous. Mixed popu-

lations of subsp. *munita* and forms approaching typical subsp. *rotundata* are not infrequent in Los Angeles Co. For further discussion of this point see the discussion of intermediates following the treatment of subsp. *rotundata*.

Many of the collections of subsp. *munita* from Baja California are quite

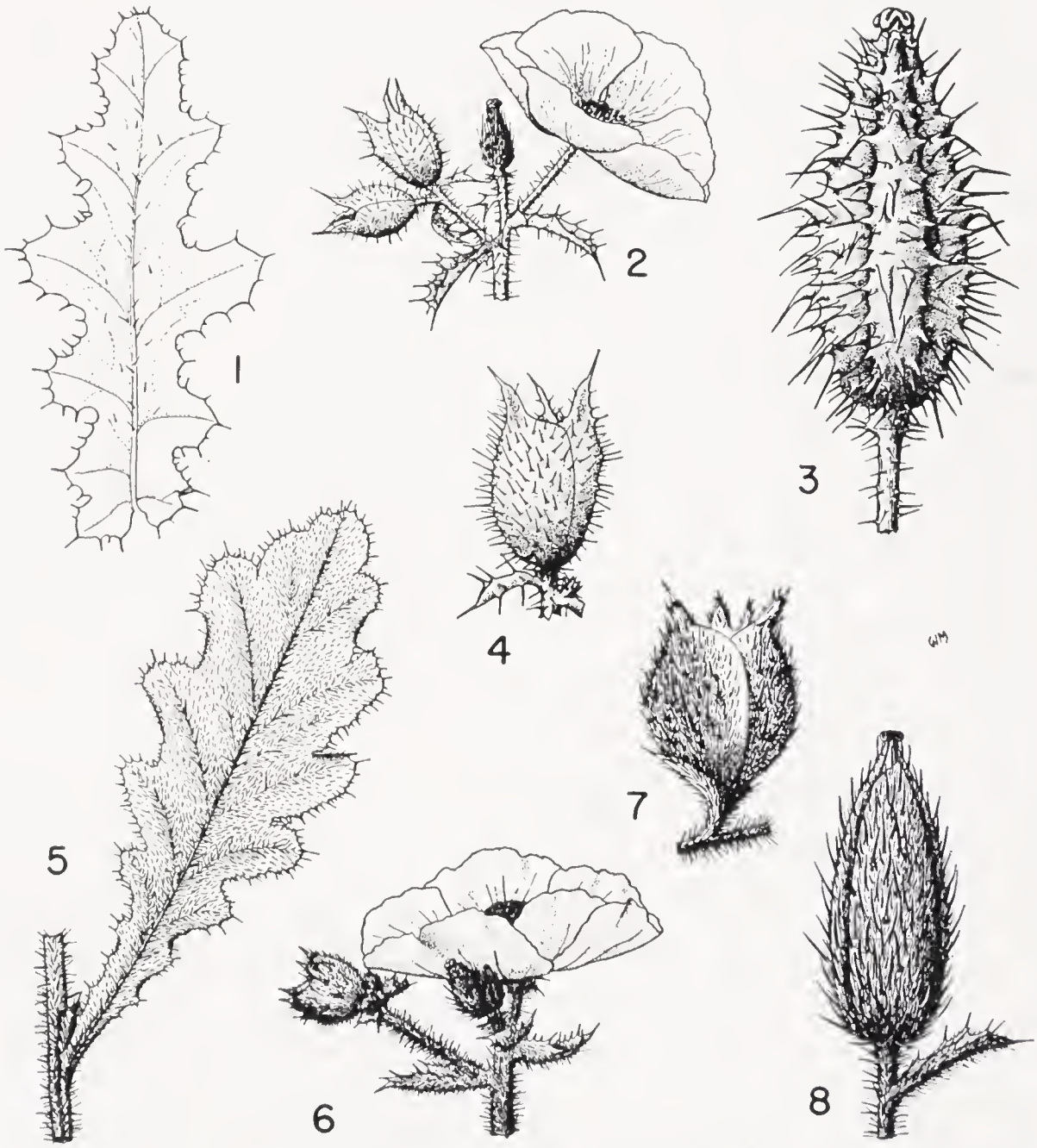

FIG. 9. 1-4. *A. munita* subsp. *munita*. 1. Middle cauline leaf × ½. *Ownbey & Ownbey* 2174 (MIN). 2. Habit × ½. Liquid preserved material of *Ownbey & Ownbey* 2174 (MIN). 3. Capsule × 1. Same as 2. 4. Bud × 1. Same as 2. 5-8. *A. munita* subsp. *rotundata*. 5. Lower surface of leaf × ½. *Lee* 720 (UC). 6. Habit × ½. Liquid preserved material of *Ownbey & Ownbey* 2179 (MIN). 7. Bud × 1. *Jones s.n.* 1897 (GH). 8. Capsule × 1. *Lee* 75 (UC).

prickly for this subspecies, but their inclusion here seems more feasible than alternative possibilities.

In Prain's monograph of *Argemone*, *A. munita* subsp. *munita* is partly included under his *A. platyceras* var. *typica* "state" β, and partly under his var. *hispida* of the same species. These are only two of the many distinct taxa included under *A. platyceras*, in the broad sense, and for a more complete enumeration of these taxa the reader should turn to the discussion of *A. platyceras* in this paper. Similarly, Fedde, in his revision, cited specimens belonging to this taxon under *A. platyceras* proper along with many other anomalous elements.

Specimens examined: UNITED STATES.

CALIFORNIA

Los Angeles Co.: Roscoe, *Eastwood* 26d (CAS); Acton, *Elmer* 3721, *in part* (MIN, NY); Mint Canyon, *Epling s.n.* (MO); Williamson's Pass, *Heermann s.n.* (PH, lectotype of *A. munita* Dur. & Hilg.); road up to Mt. Wilson from La Canada, *Jackson s.n.* (CAS); near Pasadena, *McClatchie s.n.* (NY). Riverside Co.: Idyllwild road, San Jacinto Mts., alt. 3500 ft., *Ewan* 3587 (RM); San Jacinto, *Hasse* 5664 (F, MIN, NY); Hamilton Creek, s.e. part of San Jacinto Mts., alt. 4500 ft., *Munz & Balls* 17964 (RSA); 2.8 miles s.e. of Palm Springs, *Ownbey & Ownbey* 2112 (CAS, MIN, RSA, UC, US); 0.1 mile w. of Radec, alt. 1695 ft., *Ownbey & Ownbey* 2170 (CAS, COLO, MICH, MIN, NY, POM, RM, UC, UTC, most plants possibly evidencing influences of subsp. *rotundata*); 13.2 miles s.e. of Idyllwild, Hemet Valley, alt. ca. 4500 ft., *Ownbey & Ownbey* 2178b (BM, BRY, CAS, COLO, F, GH, K, MIN, NY, POM, RM, UC, UTC, US, WS); n.w. of Dripping Springs near Temecula, *Peirson* 6015 (RSA). San Bernardino Co.: Redlands, *Woodruff s.n.* (NY). San Diego Co.: Cottonwood valley, *Abrams* 3548 (DS, F, GH, MO, NY, US); San Felipe, *Brandegee s.n.* (UC); Laguna Mts., *Brandegee s.n.* (UC); e. of Palomar Mt., *Fiker* 3657 (UC); 1.6 miles s.w. of Emory store, just e. of Palomar Mt., *Ownbey & Ownbey* 2171 (ARIZ, BM, BRY, CAS, COLO, DAO, F, GH, ILL, K, MEXU, MICH, MIN, NEW MEX, NY, OKL, RM, RSA, SMU, TEX, UC, UTC, US, WIS, WS); 3.5 miles n.e. of Laguna Jct., *Ownbey & Ownbey* 2174 (ARIZ, CAS, COLO, GH, MIN, POM, UC, UTC, US); 4 miles w. of Jacumba, alt. 3460 ft., *Wolf* 2276 (CAS, DS, GH, RSA). Santa Barbara Co.: valley of the Sisquoc River, *Baker s.n.* (UC); Cuyama, Green Canyon, *Eastwood s.n.* (GH, UC, US); Sisquoc River near Santa Maria, *Sinsheimer s.n.* (CAS). San Luis Obispo Co.: 2.5 miles s. of Round Top, Sec. 31, T. 31 S., R. 14 E., *Lee* 642 (UC). Ventura Co.: s. side of Mt. Pinos, alt. 5800 ft., *Hall* 6504 (UC); above Matilija dam, Ventura River basin, *Pollard s.n.* (CAS, RSA). County uncertain: *Fremont s.n.* (GH).

MEXICO.

BAJA CALIFORNIA

San Fernando, *Anthony s.n.* (UC); Aliso, *Brandegee s.n.* (UC); 13 km. n.w. of Rancho Mesquital *Carter, Alexander & Kellogg* 1897 (DS, UC, US); Socorro, *Orcutt s.n.* (MO); La Grulla, *Orcutt s.n.* (UC); 8.4 miles s. of Santo Tomás, *Ownbey* 2066 (MIN); Rosario Wash, *Wiggins* 5242 (CAS, DS, GH, NY, RM, UC, US); along Río Santo Domingo about 6 miles above the Mission, *Wiggins & Demaree* 4797 (DS, GH, NY, POM, UC, US); small canyon e. of the summit, 5 miles w. of Ojos Negros, *Wiggins & Gillespie* 4075 (CAS, DS, F, GH, MO, NY, POM, RSA, US).

10c. ARGEMONE MUNITA Dur. & Hilg. subsp. **rotundata** (Rydb.) G. B. Ownb., stat. nov.

A. rotundata Rydb., in Bull. Torr. Bot. Club 29: 160. 1902; Rydb., Fl. R. Mts., p. 318. 1917.

A. hispida Torrey, in Stansb., Exped. Val. Great Salt Lake, p. 383. 1852; Durand, Sketch Bot. Great Salt Lake, in Trans. Am. Phil. Soc. 11: 158. 1860; Hemsl., Biol. Cent. Am., Bot. 1: 27. 1879, as to Utah distribution only; Brew. & Wats., Bot. Calif., ed. 2, 1: 21. 1880; Britton & Brown, Ill. Fl., ed. 2, 2: 139. 1913, as to Utah distribution only; Rydb., Fl. R. Mts., p. 318. 1917, as to Utah distribution; Tidestr., Fl. Utah & Nev., in Contr. U. S. Nat. Herb. 25: 216. 1925, as to Utah & Nevada distribution; Garrett, Sp. Fl. Wasatch, ed. 5, p. 79. 1936; Peck, Man. Pl. Oregon, p. 321. 1941; not *A. hispida* Gray.

A. mexicana Torrey, in Pac. R. Rep. 5 (2) 359. 1857; not *A. mexicana* L.

A. mexicana var. *hispida* Wats., in King, U. S. Geol. Expl. Fort. Paral. 5: 13. 1871, excluding synonyms; Coulter, in Hayden, Rep. Geol. Surv. 1872: 759. 1873; not *A. mexicana* L.; not *A. hispida* Gray.

A. platyceras var. *typica* Prain, in Journ. Bot. 33: 367. 1895, in small part; not *A. platyceras* L. & O.

A. platyceras var. *hispida* Prain, l.c., in part; Eastwood, in Erythea 4: 96. 1896, as to California distribution; Abrams, Fl. Los Ang., p. 162. 1904, in part; Fedde, in Pflanzenr. 4 (104): 285. 1909, in large part; Jeps., Fl. Calif. 1: 560. 1922; Davids. & Moxl., Fl. S. Calif., p. 146. 1923, in part; Jeps., Man. Fl. Pl. Calif., p. 400. 1925; Wolf, Rancho Santa Ana Bot. Gard. Occ. Papers, ser. 1 (2): 61. 1938; Abrams, Ill. Fl., 2: 231. 1944, as to California and the Great Basin distributions; not *A. platyceras* L. & O.; not *A. hispida* Gray.

A. platyceras Fedde, in Pflanzenr. 4 (104): 283. 1909, in small part; Munz, Man. S. Calif. Bot., p. 182. 1935, in part, as to California; Abrams, Ill., Fl., 2: 231. 1944, in part; Clokey, Fl. Charles. Mts., p. 92. 1951, as to the Charleston Mts. distribution; not *A. platyceras* L. & O.

A. platyceras var. *hispida* subvar. *rotundata* Fedde, in Pflanzenr. 4 (104): 286. 1909; not *A. platyceras* L. & O.; not *A. hispida* Gray.

A. platyceras var. *hispida* subvar. *subintegra* Fedde, l.c.; not *A. platyceras* L. & O.; not *A. hispida* Gray.

A. intermedia var. *corymbosa* Jeps., Fl. Calif. 1: fig. 116. 1922, as to figure only; not *A. intermedia* Sweet; not *A. corymbosa* Greene.

Perennial with pale lemon to yellow latex; stems 1-10 (-25), 4-10 dm. tall, often purplish, moderately to densely prickly throughout (very rarely almost smooth) with uneven-sized prickles, the smallest prickles not crisped; leaves lobed, sometimes barely so, the lobes often broadly oblong and with a tendency to be rounded at the apex, marginally prickly and also more or less densely prickly above and below on the veins and intervein surfaces (very rarely almost smooth), the smallest prickles not crisped; buds oblong, 10-16 mm. broad, 14-20 mm. long, usually copiously prickly, the larger prickles often compound, i.e., with smaller secondary prickles from near the base, the sepal horns 5-8 (-10) mm. long, usually very prickly, terminated by a stout indurated spine which is generally enlarged and flattened at its juncture with the vegetative basal portion of the horn; flowers 7-12 cm. broad, the first subtending foliar bracts often several mm. distant; petals white, obovate to obcuneate; stamens 150 or more; stigmas purple, 3-5-lobed, about 3-4 mm. wide and 2.5-3.5 mm. high; capsules 3-5-carpellate, when mature, ovate to narrowly elliptical, the width, excluding the armature, 12-16 (-18) mm., the length, including the stigma and style, 30-55 mm., usually densely armed with straight or slightly incurved, usually simple spines, the largest of which seldom exceed 8 mm. in length and these occasionally with slender secondary prickles from near the base, the large spines interspersed with smaller to minute spines and prickles, the armature partially obscuring the capsular surface; seeds about 2.0-2.2 mm. broad and 2.2-2.6 mm. long. (Ill.: Fig. 9, 5-8; Dist.: Fig. 13.)

Holotype: *Sereno Watson* 47, collected in the Diamond Mountains, Nevada, alt. 6000 ft., July, 1868 (NY).

Habitat and distribution: Sandy or gravelly soil, dry, open desert slopes and foothills, low to middle elevations (mostly 4000-8500 ft.), San Bernardino Mts., southern California northward along the eastern slopes of the Sierra Nevada to Shasta Co., and localized in the coast ranges in Lake and Colusa Counties, California; northwestern Arizona and widespread in the western half of Utah, and in Nevada.

Flowering and fruiting dates: First flowers appear about May 1 in the southern parts of its range; flowering continues to about Sept. 15; fruits are matured from about July 15 to Oct. 15.

The holotype of *A. munita* subsp. *rotundata* is in the last stages of disintegration. Enough remains, however, of the leaves, stem and one bud to determine its identity beyond question. It is mounted on the same sheet as *Watson* 49, in part, from Utah Valley, Utah, which is also somewhat broken and fragmented, but which represents the same subspecies and is the only other specimen cited by Rydberg in his original diagnosis. The type has definitely rounded leaf lobes, doubtless the basis for the name, and represents an extreme expression of this tendency. The over-all prickliness of the type is also somewhat less than is found in many specimens of the subspecies from farther west. I believe that Rydberg was fully justified in describing this plant as new, since the application of the name *A. munita* Dur. & Hilg. was clouded. Further, it appeared that the leaf shape could be given considerable weight in distinguishing his species from the more westerly material which I place in the same subspecies. This position is, however, no longer tenable since individual plants in which a tendency toward rounded leaf lobes is strongly expressed are not uncommon throughout the subspecies range.

The distinguishing morphological characters of *A. munita* subsp. *rotundata* were clearly set forth by Rydberg in his original description. The most pronounced ones are: commonly quite closely prickly on both leaf surfaces, but lacking the finest, crisped surface indumentum characteristic of *A. hispida;* the tendency toward the leaf lobes to be rounded at the apex; and the ordinarily very prickly sepals.

The holotype of *A. platyceras* var. *hispida* subvar. *subintegra* Fedde, *Torrey* 10, from near Empire City, Nevada, the only collection cited in the original description, is on deposit at the Gray Herbarium. Two isotypes are at the New York Botanical Garden. The type consists of a single stem in bud, flower and early fruit. It is mounted with another specimen bearing the hand-written notation "Nevada: Dr. Anderson." Examination of the type and isotypes of this proposed subvariety makes evident that it is typical *A. munita* subsp. *rotundata* in all respects. The leaf shape upon

which it is based, falls well within the usual limits of variation for this subspecies.

Forms of *A. munita* subsp. *rotundata* which are less prickly than usual for the subspecies are found at several localities in Nevada. The most extreme example is a collection from the Toiyabe Mts. (*Linsdale & Linsdale* 474) which is essentially smooth except for prickles terminating the angles of the leaf margins. Plants classified as typical subsp. *rotundata* as well as plants intermediate in armature also occur in the Toiyabe Mts.

Specimens examined: UNITED STATES.

Arizona

Coconino Co.: Hermit Trail, Grand Canyon, *Eastwood* 5862 (CAS); same loc., *Eastwood* 5862a (CAS, GH); Nagle's Ranch (Kaibab Plateau), alt. 7600 ft., *Jones* 6054d (POM, US); near Flagstaff, alt. 1900 m., *Leiberg* 5872 (DS, US); Jacob Lake, Kaibab Plateau, *Mead* 670 (US); 14.1 miles e. of Jacob Lake in vicinity of House Rock, *Ownbey & Ownbey* 1816 (ARIZ, COLO, GH, MIN, RM, UC, UTC, US); 25.6 miles e. of Grand Canyon (village) on road to Cameron, *Ownbey & Ownbey* 1820 (MIN). Mohave Co.: 20.2 miles s.w. of Kingman, alt. ca. 1800 ft., *Ownbey & Ownbey* 2167 (ARIZ, GH, MIN, NY, RSA); Hualapai Mts., *Stephens s.n.* (UC).

California

Alpine Co.: along Carson-Markleeville Highway at state line, alt. 5000 ft., *Lee* 75 (UC); Markleeville, alt. 5500 ft., *Rose s.n.* (CAS); West Carson Canyon, alt. 6000 ft., *Yates* 3993 (UC). Colusa Co.: 1 mile e. of Mill Creek Ranger Station, alt. 1800 ft., *Constance* 2490 (CAS, DS, GH, MEXU, MIN, MO, NY, POM, RM, RSA, UC). Inyo Co.: near Independence, *Campbell s.n.* (CAS); desert slopes, lower end of Onion Valley on road to Independence, alt. 8900 ft., *Ferris* 9014 (DS, UC); Owens Valley, *Hastings s.n.* (NY); hills w. of Bigpine, *Heller* 8258 (CAS, DS, F, GH, KSC, MO, NY, US); Panamint City, Surprise Canyon, Panamint Mts., alt. 7000 ft., *Howell* 4001 (CAS); Division Creek, alt. 7000 ft., *Kerr s.n.* (CAS); Gray's Meadows, *Kerr s.n.* (CAS); s.e. base of Olancha Peak, *Straw* 683 (MIN, RSA); Sawmill Canyon, Sierras n. of Independence, alt. 5000 ft., *Train* 746 (US); Cottonwood Creek, alt. 7500 ft., *Wolf* 3244 (CAS, DS, GH, RSA). Kern Co.: near Onyx on the Walker Pass road, *Abrams* 11941 (DS, POM, UC); Kernville, *Brandegee s.n.* (UC); Caliente Creek, Huckleberry Canyon, *Brandegee s.n.* (UC); Tehachapi Mts., vicinity of Bisses Station, *Dudley* 432 (DS, NY, US); Havilah, *Grinnell* 367 (US); Walker Pass, *MacFadden* 13602 (NY); Chimney Meadow, Sec. 8, T. 24 S., R. 37 E., alt. 6000 ft., *St. John* 254 (UC); 4-5 miles s. of Tehachapi, alt. 5000 ft., *Wolf* 2189 (DS, RSA); near Monolith, Piute Mts., alt. 3800-4400 ft., *Zigmond* 6 (F). Lake Co.: north fork of Cache Creek, *Blankinship s.n.* (GH); Snow Mt., alt. 6000 ft., *Blankinship s.n.* (MO); on Eel River, 1 mile below Hullville, *Heller* 6043 (F, GH, MO, NY, UC, US); Bartlett Creek at foot of grade over Bartlett Mt., *Hoover* 3807 (UC); near Bartlett Springs, *Howell* 21210 (CAS); South Fork of the Eel River, *Jepson s.n.* (ND, UC). Lassen Co.: hills near Susanville, *Austin* 1328 (US); Milford, *Baker s.n.* (UC); near Susanville, *Eastwood & Howell* 8337 (CAS); Honey Lake, *Howell* 638 (CAS); plain in Long Valley, alt. 4500 ft., *Leiberg* 5228 (US); Doyle, *Monnet* 945 (CAS). Los Angeles Co.: Mescal Creek, San Gabriel Mts., alt. 5000 ft., *Ewan* 9934 (GH); Blue Ridge, San Gabriel Mts., alt. 8000-8500 ft., *Howell* 23416 (CAS). Mono Co.: 4.4 miles e. of Sonora Pass, alt. 7500 ft., *Albertus* 382 (UC); 2.6 miles n.w. of Rock Creek, alt. 6500 ft., *Balls & Everett* 18048 (RSA); Mono Lake, *Bolander s.n.* (GH, US); desert near Mono Lake, alt. 6450 ft., *Brewer* 1828 (US); foot of Bloody Canyon, *Chestnut & Drew s.n.* (UC); near Fales Hot Springs, alt. 7500 ft., *Constance* 2445 (GH, NY, RM, UC); 4.6 miles n.w. of Bridgeport, alt. 6700 ft.,

Graham 196 (UC); mouth of Buckeye Canyon, alt. 7000 ft., *Hendrix* 474 (UC); Mono Lake, *Jones* 24933 (GH, MO, NY, POM); 6 miles s. of Coleville, alt. 5500 ft., *Lamm* 15884 (RM); foothills near Goose Lake, *McLean s.n.* (UC); Mono Pass, *McLean s.n.* (UC); Lundy, alt. 8000-9000 ft., *Minthorn s.n.* (UC); Devil's Gate, alt. 7600 ft., *Peterson* 595 (UC); east slope of Sonora Pass, alt. 5000 ft., *Rowntree s.n.* (CAS); along Swager Creek, 9 miles n.w. of Bridgeport, alt. 6800 ft., *Wolf* 5319 (CAS, DS, POM, RSA, UC, US). Plumas Co.: n.w. end of Sierra Valley, alt. 5100 ft., *Hanks* 11 (UC); Mohawk, *Raphael s.n.* (CAS). San Benito Co.: New Idria, *Brewer* 768, *in part* (MO, UC, US). San Bernardino Co.: Lytle Creek canyon, alt. 4000 ft., *Abrams* 2692 (DS, NY, POM); Horse Springs, Kingston Mts., alt. 4200 ft., *Abrams* 14164 (DS, GH); near Coliseum Mine, Clark Mt., alt. 4800 ft., *Alexander* 479 (UC); 1.5 miles n.w. of mouth of Deep Creek, alt. 2950 ft., *Axelrod* 520 (UC); Lytle Creek canyon, alt. 4500 ft., *Hall* 1428 (UC); Johnson Grade, just n. of Baldwin Lake, alt. ca. 6900 ft., *Ownbey & Ownbey* 2129 (MIN, NY, RM, RSA, UC); 2.0 miles w. of Cajon Junction, *Ownbey & Ownbey* 2168 (ARIZ, BM, BRY, CAS, COLO, DAO, F, GH, ILL, K, MEXU, MICH, MIN, NEW MEX, NY, POM, RM, SMU, TEX, UTC, US, WIS, WS); hills near San Bernardino, *Parish s.n.* (NY); Hesperia, alt. 3100 ft., *Spencer* 420 (GH, NY, POM); San Bernardino Mts., *Vasey* 16 (F); Clark Mt., 0.5 mile n.w. of Coliseum Mine, alt. 5000 ft., *Wolf* 9599 (RSA, UC); Horse Thief Spring, Kingston Mts., alt. 4768 ft., *Wolf* 9694 (RSA, UC). Shasta Co.: stage road near Hat Creek, *Baker* 391 (UC); west of Fall River Mills, *Cantelow* 1048 (CAS); Pitt River Canyon, *Eastwood* 1055 (CAS). Sierra Co.: Loyalton, *Eastwood* 7825 (CAS, US); 3.8 miles s.e. of Dog Valley, alt. 5000 ft., *Nordstrom* 937 (UC); road to Reno near inspection station, *Schreiber* 883 (UC). Tulare Co.: Kern Flats, *Baker* 4556 (coll. by Culbertson) (GH, MO, ND, POM).

Nevada

Churchill Co.: East Gate, alt. 5100 ft., *Allen* 363 (DS, NY); same loc., *Allen* 364 (MO). Clark Co.: near Cold Creek, Charleston Mts., alt. 6000 ft., *Burt* 2 (UC); Charleston Park, Charleston Mts., alt. 2270 m., *Clokey* 5472 (CAS, F, GH, ND, NY, RM, RSA, UC, US); Kyle Canyon, Charleston Mts., alt. 2100 m., *Clokey* 7927 (DS, F, GH, KSC, MIN, MO, ND, NY, POM, RM, RSA, TEX, US). Douglas Co.: between Carson and Smith valleys, *Lehenbauer* 138 (NY). Elko Co.: 10 miles n. of Ruby Valley Store, *Holmgren* 1256 (NY, UC). Esmeralda Co.: Tule Canyon, south of Lida, alt. 1500 m., *Tidestrom* 9821 (MO). Lander Co.: Big Creek, Toiyabe Mts., *Linsdale & Linsdale* 331 (CAS); Birch Creek, Toiyabe Mts., *Linsdale & Linsdale* 474, 475 (CAS), less prickly form. Lincoln Co.: near Utah line e. of Panaca, *Eastwood & Howell* 7313 (CAS); Mormon Mts., alt. 3000-6000 ft., *Kennedy & Goodding* 109 (NY, UC, US); 9.5 miles w. of Caliente, alt. ca. 6500 ft., *McVaugh* 5982 (UC); Pioche, alt. 6500 ft., *Minthorn s.n.* (UC); Caliente, alt. 1320 m., *Tidestrom* 9535 (NY, US). Lyon Co.: 2 miles e. of Dayton, *Goodner & Henning* 80 (MO); Smith Valley, *Haley s.n.* (CAS). Mineral Co.: Corey Canyon, Wassuk Mts., alt. 1600 m., *Tidestrom* 10077 (NY). Nye Co.: Grime's ranch near Monitor Range, alt. 1820 m., *Tidestrom* 10986 (US). Ormsby Co.: Eagle Valley near Carson, alt. 1446 m., *Baker* 1090 (GH, MO, ND, NY, POM, RM, UC, US); near Empire City, *Torrey* 10 (GH, holotype of *A. platyceras* var. *hispida* subvar. *subintegra* Fedde; isotype, NY). Storey Co.: near Virginia City, *Bloomer s.n.* (US); Geiger Grade to Virginia City, *Eastwood* 14824 (CAS). Washoe Co.: Reno, alt. 5500 ft., *Jones s.n.* (DS, GH, POM, US); 1 mile w. of Steamboat Springs, *McVaugh* 6135 (UC); 8 miles n. of Poeville, alt. 5250 ft., *Tillotson* 109 (UC). White Pine Co.: Warm Springs, *King s.n.* (CAS); 18.6 miles n.w. of Ely on U. S. Hwy. 50, *McVaugh* 6104 (UC); mesa w. of Baker, alt. 1950 m., *Tidestrom* 11137 (MO). County uncertain: Diamond Mts., alt. 6000 ft., *Watson* 47 (NY, holotype of *A. rotundata* Rydb.); Pah-Ute Mts., alt. 5000 ft., *Watson* 49, in part (US).

Utah

Beaver Co.: 4 miles s. of Minersville, Mineral Mt., *Harris* C29212 (MIN, UC); Milford, alt. 5000 ft., *Jones* 1605 (NY, POM). Box Elder Co.: foothills e. of Brigham,

Zundel 212 (DS, NY). Davis Co.: Farmington Canyon, *Garrett* 7641 (KANU). Iron Co.: Cedar City, alt. 6000 ft., *Ballow s.n.* (DS, RM). Juab Co.: Juab, *Goodding* 1055 (GH, MO, NY, POM, RM, UC, US). Kane Co.: mouth of Clear Creek Canyon, Zion National Park, alt. 5700 ft., *Boyle* z152 (UC). Millard Co.: 7 miles s. of Kanosh, alt. 5450 ft., *Barkley & Reed* 4039 (GH, NY, POM). Piute Co.: Marysvale, alt. 6000 ft., *Jones* 5388a (NY, UC, US); along Sevier River below Marysvale, *Rydberg & Carlton* 6975 (NY, RM, US). Salt Lake Co.: near Salt Lake City, *Garrett* 1824 (RM); Bacchus, *Jones s.n.* (UC). Sanpete Co.: Manti, alt. 6000 ft., *Jones* 5516 (MO, POM, US); near Ephraim, alt. 1650 m., *Tidestrom* 140 (US). Sevier Co.: Clear Creek Canyon, *Garrett* 2516 (NY); Glenwood, alt. 5300 ft., *Ward* 189 (US). Tooele Co.: Grantsville, *Garrett* 2765 (GH). Utah Co.: Santaquin, *Eastwood & Howell* 580 (CAS); Lehi, *Jones* 99 (GH); Lehi, *Jones s.n.* (UC); Utah Valley, alt. 5000 ft., *Watson s.n., in part* (NY). Washington Co.: near Sugar Loaf Butte, St. George, *Degener & Peiler* 16396 (RM); Diamond Valley, 11 miles n. of St. George, alt. 3500 ft., *Gould* 1799 (GH, NY, UC, US); 10 miles e. of Leeds, *Hitchcock* 3035 (UC); 20 miles n.e. of St. George, alt. 4000 ft., *McKelvey* 4186 (GH); Leeds, *Tidestrom* 9400 (GH, NY, US). Weber Co.: Ogden Canyon, Ogden, alt. 5000-6000 ft., *Pammel & Blackwood* 3752 (CAS, GH, MO).

10d. Argemone munita Dur. & Hilg. subsp. munita X A. munita subsp. rotundata (Rydb.) Ownb.

A. munita Greene, Fl. Franc., p. 281. 1892.

A. platyceras Wolf, in Rancho Santa Ana Bot. Gard. Occ. Papers, ser. 1 (2): 60. 1938, in small part; not *A. platyceras* L. & O.

A. platyceras var. *hispida* Bower., Fl. Pl. Mt. Diablo, p. 151. 1944; not *A. platyceras* L. & O.; not *A. hispida* Gray.

Transitional forms between subsp. *munita* and subsp. *rotundata* create the greatest taxonomic difficulties. No attempt is made herein to assign true intermediates to any subspecies and no nomenclatorial category designed to include these intermediates is proposed since both alternatives are unsound and, practically speaking, appear impossible. Some statements concerning the distributional relationships of subspp. *munita* and *rotundata* and their intermediates may be made, however, with some assurance. Subsp. *munita* is found in northern Baja California and along the coastal ranges of southern California as far north as San Luis Obispo County. Subsp. *rotundata* is found from the San Bernardino and San Gabriel mountains northward along the eastern slopes of the Sierra Nevada where it reaches its most typical state, to Shasta and Lassen Counties, California. It occurs eastward across the southern two-thirds of Nevada and the western half of Utah at intermediate elevations. Outlying occurrences of nearly typical subsp. *rotundata* are in Lake and Colusa Counties, and in San Benito County, California.

Distributionally, subsp. *rotundata* impinges upon subsp. *munita* in the San Bernardino and San Gabriel Mts. of southern California. Commonly in this area and along the coastal ranges northward in California more or less intermediate forms occur (Dist.: Fig. 13). It is postulated that at least part of these intermediates, especially those from western Riverside, western San Bernardino, and Los Angeles Counties are hybrid derivatives

of the two subspecies. The series of intergrading forms found here is continuous, and the morphologieal characters of the two subspecies are recombined to varying degrees. Mixed populations containing individuals which would be classified as subsp. *munita* and other individuals which would be classified as intermediates or whieh approach subsp. *rotundata* are not uncommon. Very detailed analyses of representative natural populations of *A. munita* from the above area in field, garden and laboratory are needed in order to elarify the picture. It is certain that genetic factors not now understood are influencing the variability of this species.

Specimens examined of intermediate character between *A. munita* subsp. *munita* and *A. munita* subsp. *rotundata:* UNITED STATES.

California

Contra Costa Co.: Mitchell Canyon, Mt. Diablo, *Bowerman* 1603 (UC). Fresno Co.: White Creek, Sec. 25, T. 19 S., R. 13 E., alt. 1600 ft., *Johannsen* 67 (UC). Kern Co.: Ft. Tejon, alt. 3200 ft., *Abrams & McGregor* 279 (DS, NY, US); Ft. Tejon, *Horn s.n.* (NY, US); Rosamond, *Weston s.n.* (CAS). Los Angeles Co.: Bouquet Canyon, alt. 600 m., *Clokey, Clokey & Templeton* 4614 (UC); Acton, *Elmer* 3721, *in part* (GH, MO, POM, US); Bald Flat on Blue Ridge, San Gabriel Mts., alt. 8300 ft., *Ewan* 10024 (GH); San Francisquito Canyon, *MacFadden* 72E (RM, UC); 14 miles s. of Vincent on road to La Canada, *Ownbey & Ownbey* 2116, *in part* (MIN, RSA, UC); Soledad Canyon, 7 miles w. of Ravenna, *Ownbey & Ownbey* 2118 (BM, BRY, CAS, COLO, F, GH, MIN, RM, RSA, SMU, UC, WS); San Francisquito Canyon, 8.8 miles n. of Saugus, *Ownbey & Ownbey* 2121 (CAS, GH, MIN, RSA, UC, US); 1.9 miles s.e. of Valyermo P. O., *Ownbey & Ownbey* 2122 (MIN, NY, POM, UTC); one-half way between Castaic and Sandberg, Libre Mts., *Wolf* 2184 (DS, RSA, US). Riverside Co.: between Beaumont & Riverside, *Winblad s.n.* (CAS). San Benito Co.: New Idria, *Brewer* 768, in part (GH, US); San Benito, *Eastwood* 6926 (CAS). San Bernardino Co.: head of Clark's Grade, San Bernardino Mts., alt. 7700 ft., *Munz* 10583 (POM, UC); San Bernardino, alt. 1000-2500 ft., *Parish* 4684 *or* 4784 (DS, NY, US); foothills of San Bernardino Mts., *Parish & Parish* 128 (DS, NY, US). San Diego Co.: Hell Hole Canyon near Borego, *Epling & Robison s.n.* (DS, MO, NY); Jacumba Hot Springs near Monument 233, *Schoemfeldt* 3256 (US). Santa Barbara Co.: Bates Canyon, Sec. 18, T. 10 N., R. 28 W., alt. 3200 ft., *Freneh* 783 (UC); Cuyama Valley, Sec. 18, T. 9 N., R. 24 W., alt. 2800 ft., *Sowder* 410 (UC). Stanislaus Co.: Arroyo del Puerto, Mt. Hamilton Range, alt. 1350 ft., *Sharsmith* 3776 (DS, UC). Tehama Co.: burned area, mountains, alt. 800 ft., *Bertin s.n.* (CAS). Ventura Co.: upper Sespe Creek n. of Wheeler's Hot Springs, alt. 3500 ft., *Munz* 13223, 13233 (POM, UC).

10e. Argemone munita Dur. & Hillg. subsp. **argentea** G. B. Ownb., subsp. nov.

A. platyceras Coville, Bot. Death Valley Exped., in Contr. U. S. Nat. Herb. 4: 59. 1893; Eastwood, in Erythea 4: 96. 1896, in small part; Jeps., Fl. Calif. 1: 560. 1922, in part, as to California; Jeps., Man. Fl. Pl. Calif., p. 399. 1925, in part, as to California; Munz, Man. S. Calif. Bot., p. 182. 1935, in part, as to California; Wolf, in Rancho Santa Ana Bot. Gard. Occ. Papers, ser. 1 (2): 60. 1938, in small part; not *A. platyceras* L. & O.

Herba perennis. Caules 1-15 vel plus, fruticosissimi, longis et tenuibus aculeis dense muniti. Folia inferiora lobata, lobis circiter tam latis quam longis, apice rotundata, marginibus dense dentatis, superficibus plerumque aculeis longis et patentibus munitis. Alabastra elliptico-oblonga aculeatissima. Flores 5-8 cm. diametro, petalis albis, sta-

minibus circa 200. Capsulae 3 (-5) -carpellatae, elliptico-lanceolatae vel lanceolatae, multis spinis magnitudine inaequali et aculeis armatae. Semina 1.8-2.2 mm. longa.

Perennial with very pale lemon-yellow, nearly white, latex; stems 1-15 or more from the base, 4-8 dm. tall, very bushy, often copiously branched, mostly closely armed with long, slender, perpendicular prickles, greenish-white throughout; leaves very glaucous, oblanceolate below to progressively elliptical to ovate-lanceolate upward, the uppermost partially clasping the stem, the lowermost to about 2 dm. long, lobed to about one-half or more of the distance to the midrib, the lobes rounded apically, about as broad as long, the sinuses narrow, the middle and upper leaves progressively more shallowly lobed, the uppermost often very shallowly and irregularly lobed, the leaf margins irregularly dentate, the teeth mostly close set and each terminated by a stout prickle, both surfaces of the leaves usually copiously armed with long, spreading prickles; buds elliptic-oblong, 10-15 mm. wide, 12-18 mm. long, copiously beset with slender, simple, ascending prickles, the sepal horns terete in cross-section, 4-6 (-10) mm. long including the terminal spine, prickly; flowers 5-8 cm. in diameter when fully expanded, often separated by several mm. from the nearest subtending foliar bract; petals white, obcuneate to obovate; stamens numerous, about 200 or more, about equalling the pistil in length at anthesis, the anthers yellow, the filaments lemon-yellow; stigma purple, about 2.5-3.0 mm. wide and 2.0-2.5 mm. high, usually 3 (-5) -lobed; style evident in fruit, 1-2 mm. long; capsules usually 3 (-5) -carpellate, elliptic-lanceolate to lanceolate, the width, exclusive of spines, 10-14 mm., the length, including the stigma and style, 25-35 mm., the armature consisting of numerous uneven-sized spines and prickles, the longest of which is about 6-8 mm., the capsular surface partially obscured; seeds about 1.8-2.2 mm. long. (Ill.: Fig. 10, 1-3; Dist.: Fig. 13.)

Holotype: *Ownbey & Ownbey* 2113, collected 0.5 mile s.w. of Beal Well, Chocolate Mts., Imperial Co., Calif., May 22, 1954 (MIN; isotypes, ARIZ, BM, BRY, CAS, COLO, F, GH, K, MICH, MIN, MO, NEW MEX, NY, RM, RSA, SMU, UC, UTC, US, WS).

Habitat and distribution: Along washes, sandy or decomposed granitic soils, in and adjacent to the dry desert mountain ranges of southern California, Death Valley and adjacent Arizona and southern Nevada, at altitudes of 1500 ft. or less in the south to 3000 ft. or more in the north.

Flowering and fruiting dates: First flowers appear about March 1, the last in late May or early June; fruits mature from about April 15 to July 15, but in greatest abundance in late May and June.

Plants of this subspecies are usually copiously prickly on the stems with long, slender, perpendicular prickles. The long prickles are interspersed with comparatively few minute prickles. The prickles of the buds are ascending, simple, and comparatively soft; the sepal horns usually are short and broad at the base. These and other features lead me to believe that subsp. *argentea* is sufficiently distinct from subsp. *rotundata* to merit taxonomic recognition. The geographical distributions of the two are completely disjunct; subsp. *argentea* grows in more arid habitats at low elevations. The possibility of genetic interchange between migrant individuals of the two taxa, however, still exists.

A. munita subsp. *argentea* is abundant at Beal Well and for a few miles along the road through the pass southwestward towards Niland. The plants

FIG. 10. 1-3. *A. munita* subsp. *argentea*. 1. Habit × ½. *Ownbey & Ownbey* 2073 (MIN). 2. Bud × 1. Same as 1. 3. Capsule × 1. Holotype, *Ownbey & Ownbey* 2113 (MIN). 4-5. *A. munita* subsp. *robusta*. 4. Buds × 1. Liquid preserved material of topotype, *Ownbey & Ownbey* 2177 (MIN). 5. Capsules × 1. Same as 4.

in this area are most typical of the subspecies as I understand it, and for this reason I have chosen Beal Well as the type locality.

Specimens examined: UNITED STATES.

ARIZONA

Mohave Co.: foot of Needles, Colorado River, *Grinnell s.n.* (UC). County uncertain: spring near Pierce's Ferry alt. 1700 ft., *Jones* 5077a (POM); near mouth of Bill Williams Creek, *MacDougal* 26 (NY).

CALIFORNIA

Imperial Co.: between Chuckwalla Well and Niland, Colorado Desert, alt. ca. 850 ft., *Jaeger* 819 (US); Beal Well, *Munz* 11940 (POM, UC); 12 miles e. of Niland on road to Beal Well, *Ownbey* 2073 (GH, IA, ILL, IND, KSC, MIN, NY, OKL, US, WIS); 0.5 mile s.w. of Beal Well, Chocolate Mts., *Ownbey & Ownbey* 2113 (MIN, holotype of *A. munita* Dur. & Hilg. subsp. *argentea* Ownb.; isotypes, ARIZ, BM, BRY, CAS, COLO, F, GH, K, MICH, MIN, MO, NEW MEX, NY, RM, RSA, SMU, UC, UTC, US, WS); "Fort Yuma, Cal.," *Thomas s.n.* (NY); 8.7 miles n.e. of Niland on road to Beal Well and Blythe, *Wiggins* 9619 (DS, GH, UC); 13 miles from Niland on road to Beal Well, alt. 600 ft., *Wolf* 1876 (DS, RSA, UC). Inyo Co.: canyon near Darwin Falls, Argus Mts., alt. ca. 2500 ft., *Ferris* 7416 (DS NY, POM); Grapevine Canyon, n.e. entrance to Death Valley, 1.0-1.5 miles above Scotty's Castle, alt. ca. 3200 ft., *Straw* 899 (CAS, GH, MIN, NY, RM, UC, US); Titus Canyon, Grapevine Mts., n.e. side of Death Valley, alt. ca. 3000-4000 ft., *Straw* 900 (ARIZ, BM, CAS, COLO, F, GH, MIN, NY, UC, US, UTC); Trail Canyon, Panamint Range, s.w. side of Death Valley, Furnace Creek Quadrangle, alt. ca. 3000 ft., *Straw* 901 (MIN); Johnson Canyon, Panamint Range, Bennetts Well Quadrangle, alt. ca. 3000 ft., *Straw* 902 (GH, MIN, US); Townes Pass road, w. side of Panamint Range, Panamint Butte Quadrangle, alt. ca. 4100 ft., *Straw* 903 (CAS, GH, MIN, UC, US); Hopkins Ranch, Surprise Canyon, Panamint Mts., Telescope Peak Quadrangle, alt. 3000 ft., *Wolf & Johnson* 8763 (DS, RSA). Riverside Co.: Chuckwalla Mts., *Hall* 5970 (UC); south base, Pinto Mts., road Dale to Cottonwood Springs, alt. 2000 ft., *Munz* 15675 (DS, POM); Desert Center, *Nelson & Nelson* 3341 (DS, RM, SMU, UC); Hayfield, 37 miles e. of Indio, *Rose* 36828 (CAS); Mecca-Blythe road, ¾ mile w. of Utopia, alt. ca. 500 ft., *Wolf* 3038 (CAS, DS, RSA, UC, US). San Bernardino Co.: north side of Whipple Mts., alt. 950 ft., *Alexander & Kellogg* 1223 (GH, UC); Bagdad, *Brandegee s.n.* (UC); Copper Basin Creek, Whipple Mts., *Peirson* 11478 (RSA). San Diego Co.: Split Mt., Colorado Desert, *Brandegee s.n.* (UC).

NEVADA

Clark Co.: stony slopes, Las Vegas Mts., *Goodding* 2357 (GH, MO, RM).

11. ARGEMONE **subintegrifolia** G. B. Ownb., sp. nov.

A. platyceras var. *hispida* Johnston, in Proc. Calif. Acad. 12: 1025. 1924; not *A. platyceras* L. & O.; not *A. hispida* Gray.

Herba perennis. Caules sublignosi albi annui. Folia siccana coriacea glaucissima, foliis cauliuis ellipticis non lobatis, in marginibus irregulariter dentata, superficibus regulariter aculeatis dispersis et rigidis aculeis. Alabastra oblonga. Sepalorum cornua brevia lataque 4-5 mm. longa. Flores 8-10 cm. diametro, 2-4 bracteis foliaribus subtensi, petalis albis. Capsulae 5-6-carpellatae, ovatae, deuse spinescentes. Semina circa 1 mm. longa.

Stout perennial, the latex color unknown; stems 3-12 dm. tall, sparingly branched near the top, the branches annual, subligneous, white, armed throughout with rather close-set, long, rigid, perpendicular prickles; leaves coriaceous when dry, very glaucous, the basal ones unknown, the middle cauline to 10 cm. long, gradually reduced upward, elliptical, unlobed, the margin sometimes undulate, irregularly toothed, each tooth terminated by a prickle, the lower and upper surfaces evenly prickly with scattered,

long, rigid, erect prickles; buds broadly oblong, the body 15-17 mm. broad, 22-25 mm. long, abundantly prickly with slender, ascending prickles, the sepal horns short and broad, 4-5 mm. long including the terminal spine, prickly; flowers 8-10 cm. in diameter, closely subtended by 2-4 large foliar bracts; petals white, obovate to obcuneate; stamens numerous; stigma purple, about 3-4 mm. broad and 3 mm. high, sessile; capsules 5-6-carpellate, ovate, broadest near the base, the width, excluding the armature, 13-15 mm., the length, including the stigma, 25-30 mm., densely spinescent with small, ascending spines, the longest spines about 5-6 mm., the capsular surface barely visible through the armature; seeds just over 1 mm. long. (Ill.: Fig. 11, 1-2; Dist.: Fig. 13.)

Holotype: *C. Epling, M. Darsie, Wm. Steward & Wm. Robison s.n.*, from the western base of the Cocupah Mts., on the shores of Laguna Macuata, Feb. 19, 1933 (US; isotypes, DS, F, MO, NY, POM, RSA, UC).

Habitat and distribution: Rocky soils, northeastern Baja California and Angel de la Guarda Island, at elevations of near sea level.

Flowering and fruiting dates: First flowers appear by February 1; fruits are matured in March, April and May.

This species may be distinguished by its unlobed, dentate-margined, elliptical leaves, rigid, erect prickles on the leaf surfaces, white stems, short sepal horns, large flowers, large, sessile stigmas, rather densely spinescent capsules each with 5 or 6 carpels, and small seeds. It appears to be fully distinct from all other species of *Argemone*.

Dr. I. M. Johnston who first collected the species in 1921 noted upon his herbarium labels that it was probably new. I have, however, taken the specimens procured by Epling and his companions in 1933 as the type collection, since this collection is more widely distributed and shows the plants at an earlier and more representative stage of growth.

In his discussion of his collection, Johnson (1924) refers it to *A. platyceras* var. *hispida* (Gray) Prain with great reservation: "To this species is doubtfully to be referred a very peculiar collection made at the lagoon on Angel de la Guarda Island (3398). The specimens came from a small colony growing on an outcrop at the edge of an elevated mesa somewhat back from the shore. The plant had a woody caudex 3-6 dm. high upon which were borne the ascending simple stems of the year, these about 6 dm. long. Fruit, but no flowers, was found. The leaves are glaucous, aculeate, with shallow teeth, and are oblong in shape and narrowed towards the base. The shrubby character of the plant is very peculiar, but due to the lack of flowers, the plant is not named here." If I am correct in placing Johnston's collection in *A. subintegrifolia* the deficiency in flowering specimens is met. Johnston's observations are of the utmost value since he is the only botanist who are carefully observed the species in the field.

Specimens examined: MEXICO.

Baja California

Western base of Cocupah Mts. on shores of Laguna Maguata (i.e., Laguna Macuata

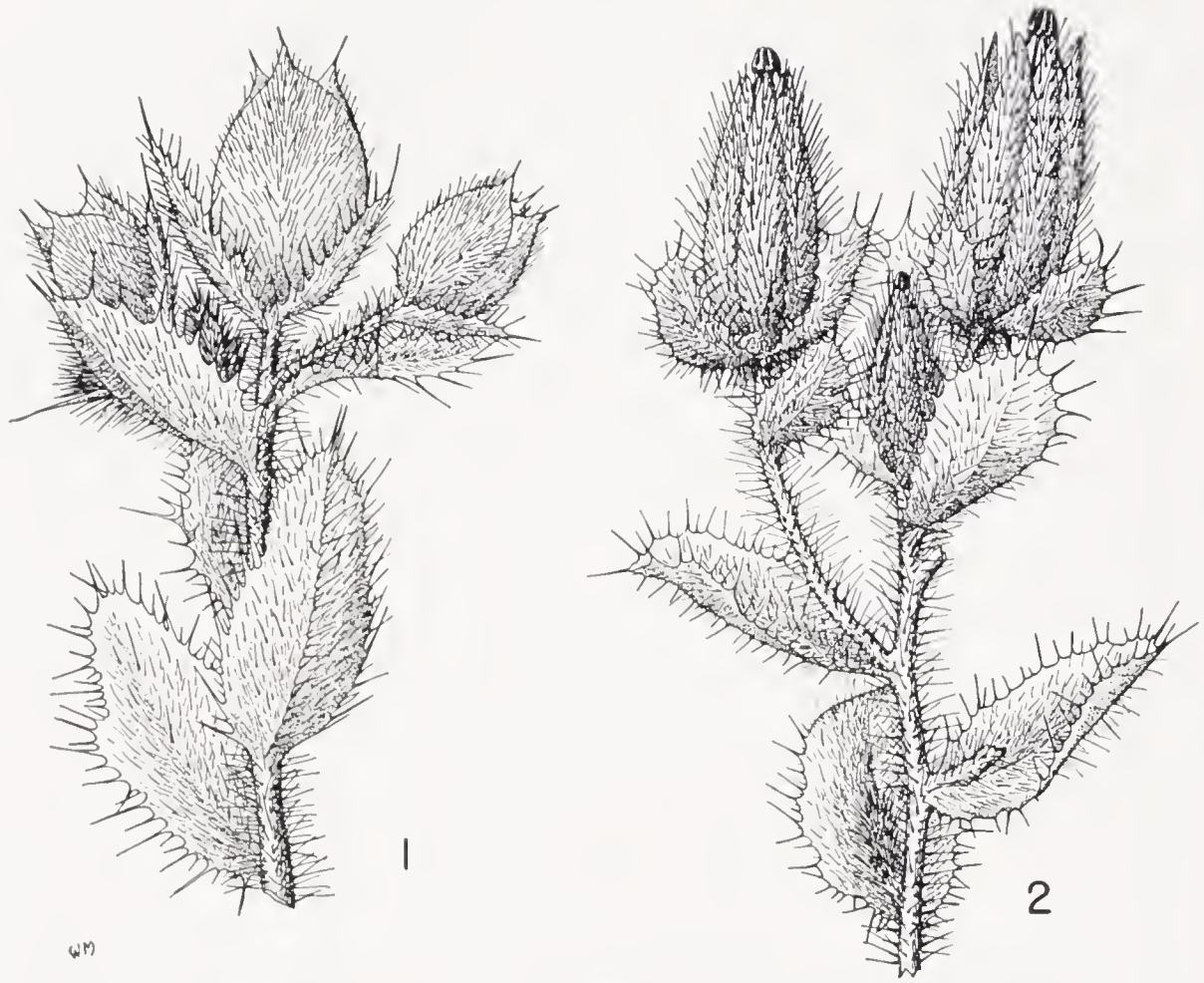

FIG. 11. *A. subintegrifolia*. 1. Stem with buds × 1. Holotype, *Epling et al. s.n.* (US). 2. Stem with capsules × 1. *Johnston* 3398 (CAS).

or Salada), *Epling et al. s.n.* (US, holotype of *A. subintegrifolia* Ownb.; isotypes, DS, F, MO, NY, POM, RSA, UC); The Lagoon, Angel de la Guarda Island, *Johnston* 3398 (CAS; GH, photograph; US, fragments and photograph).

12. ARGEMONE **brevicornuta** G. B. Ownb., sp. nov.

Herba perennis latice fulvo. Caules 3-5 dm. alti, dense aculeati. Alabastra subsphaerica, 12-14 mm. lata, 13-15 mm. longa, aculeis circa 2-3 mm. longis. Sepalorum cornua 3-5 mm. longa. Flores 7-9 cm. diametro, petalis albis, staminibus 150 vel plus, filamentis citro-flavis, antheris luteis. Capsulae 3-4-carpellatae, anguste elliptico-lanceolatae, 8-10 mm. latae, 25-35 mm. longae, spinibus sparsis magnitudine irregulari armatae. Semina circa 2 mm. longa.

Perennial with bright yellow latex; stems 1-several, 3-5 dm. tall, sparingly branched from the middle upward, rather copiously prickly with slender, perpendicular prickles; lower leaves often lobed to four-fifths of the distance to the midrib, the upper ones more shallowly lobed, the larger lobes oblong, the leaf margins with acute, prickle-tipped teeth, the leaf surfaces sparsely to copiously prickly below, prickly only on the main veins above; buds subspherical, 12-14 mm. broad, 13-15 mm. long, distinctly short prickly, these mostly 2-3 mm. long, the sepal horns comparatively short, 3-5 mm. in length, the weak, indurated apical spine sometimes visibly flattened; flowers 7-9 cm. in diameter, closely subtended by 1-2 foliar bracts; petals white, obovate-obcuneate; stamens about 150 or more, the filaments lemon yellow, the anthers yellow; stigma purple, 2.5-3.5 mm. wide, 1.5-2.5 mm. high; capsules 3-4-carpellate, narrowly elliptic-

lanceolate, the width, exclusive of armature, 8-10 mm., the length, including the stigma 25-35 (-40) mm., the surface armed with scattered, larger spines interspersed with smaller spines and prickles, the largest spines to 5-6 mm. long, the capsular surface clearly visible through the armature; seeds about 2 mm. long. (Ill.: Fig. 12, 1-4; Dist.: Fig. 13.)

Holotype: *Gerald B. Ownbey & Findley Ownbey* 1462, collected on rocky hillsides, dry soil, 23 miles n.w. of Meoqui on road to Chihuahua, Chihuahua, Mexico, July 29, 1950 (MIN; isotype, MIN).

Habitat and distribution: Gravelly soil, hills and intermountain plains, chaparral province, southern Chihuahua, Mexico, at altitudes of about 4000 to 5000 feet.

Flowering and fruiting dates: Limited data indicate that this species flowers from June to October or later and fruits from July to November.

This species is distinguished by its stem armature which generally consists of an abundance of long and slender perpendicular prickles, by its

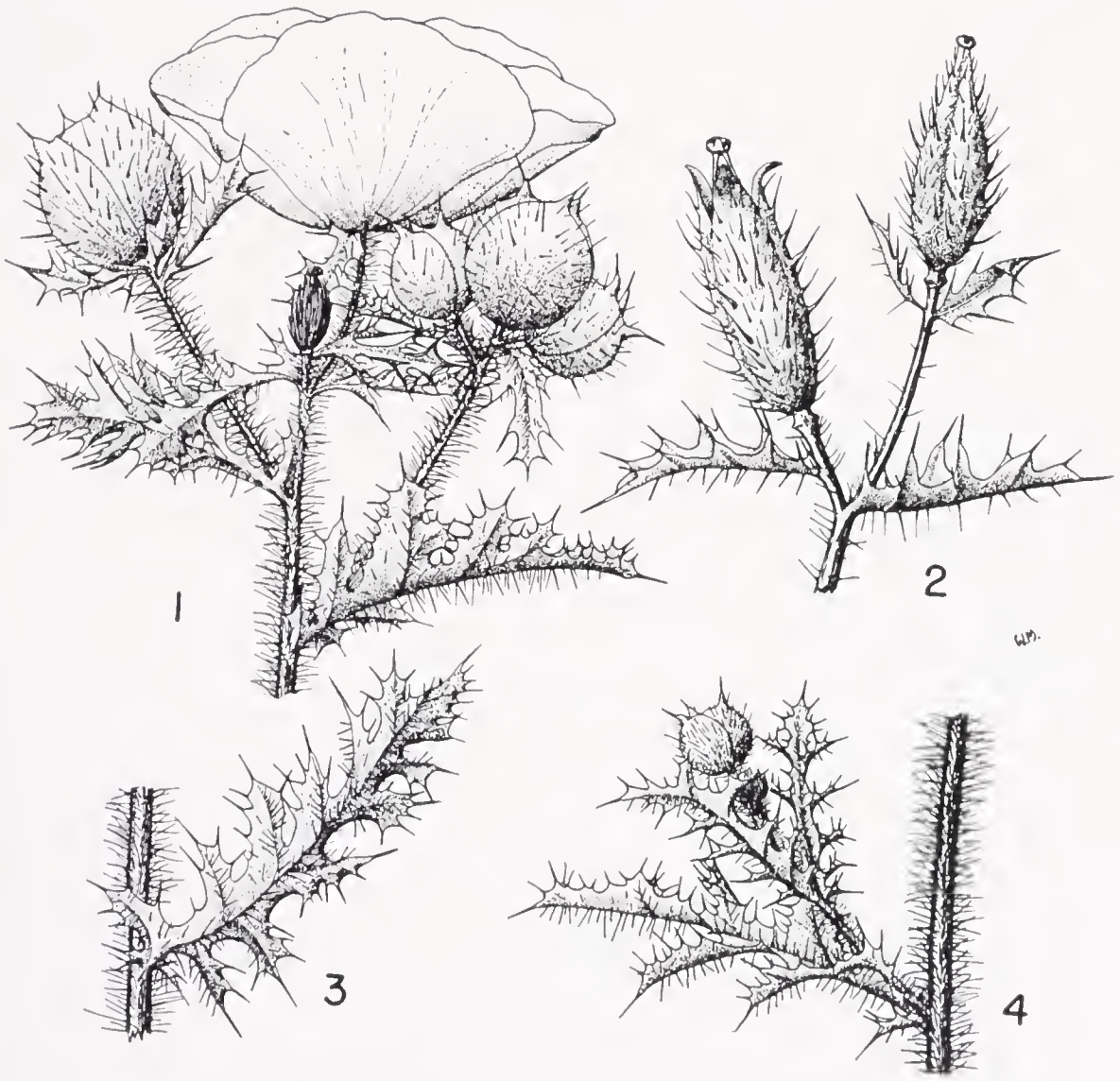

FIG. 12. *A. brevicornuta.* 1. Habit × 1. Holotype, *Ownbey & Ownbey* 1462 (MIN). 2. Capsules × 1. *Ownbey & Ownbey* 1845 (MIN). 3. Cauline leaf × 1. Same as 1. 4. Young branch × 1. Same as 1.

buds which are subspherical and distinctly short-prickly, and by its very short sepal horns. The buds are unlike those found in any other species of *Argemone*.

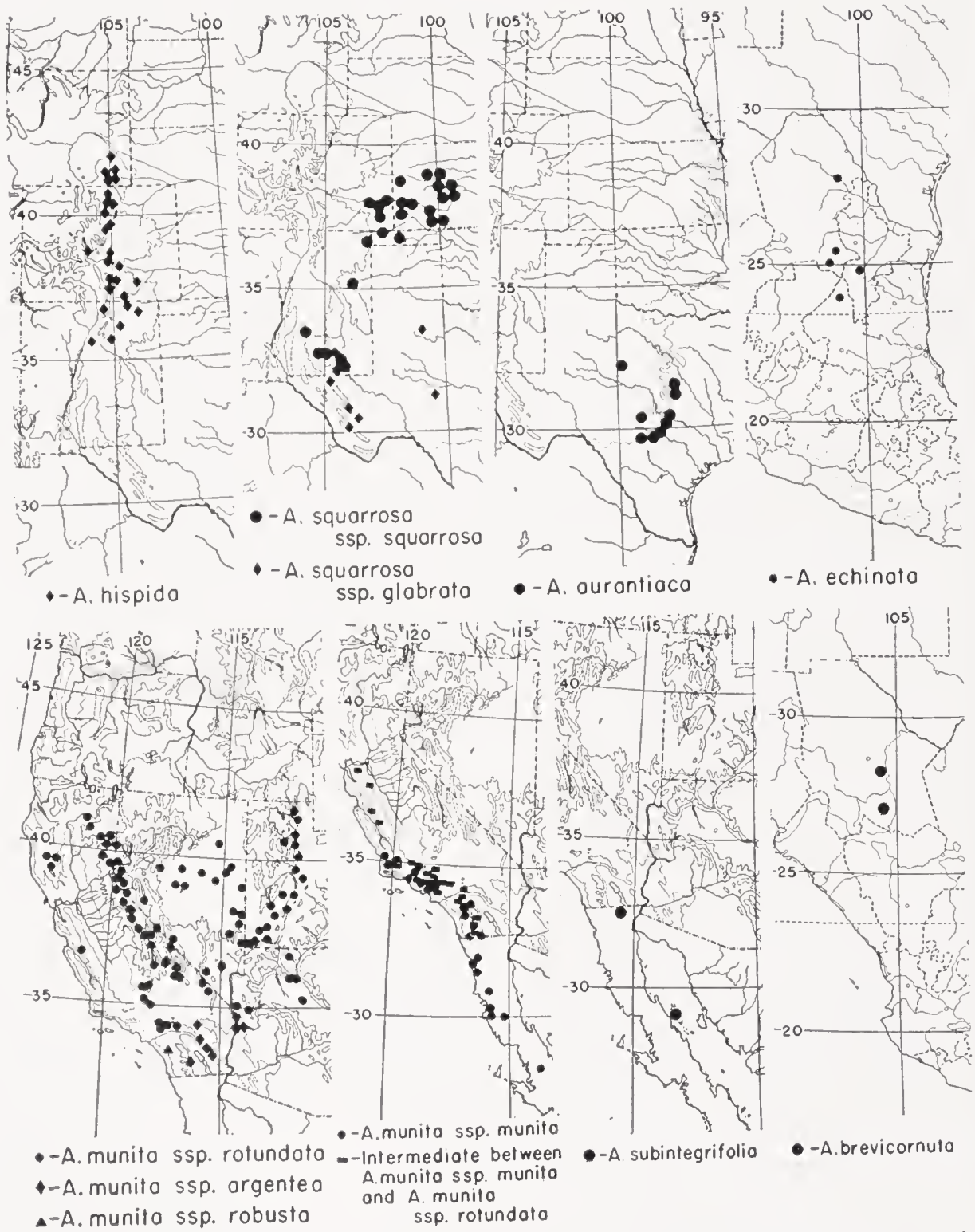

FIG. 13. Geographical distributions of species, subspecies and intermediates as indicated.

Specimens examined: MEXICO

CHIHUAHUA

Twenty-three miles n.w. of Meoqui, *Ownbey & Ownbey* 1462 (MIN, holotype of *A. brevicornuta* Ownb.; isotype, MIN); 17.3 miles n.w. of Meoqui, *Ownbey & Ownbey* 1845 (CAS, K, MICH, MIN, POM); 13.2 miles n.w. of Meoqui, *Ownbey & Ownbey* 1846 (ARIZ, F, GH, MEXU, MIN, MO, NY, UC, US); 19.6 miles e. of Hidalgo del Parral, *Ownbey & Ownbey* 1848 (MIN).

13. ARGEMONE **arizonica** G. B. Ownb., sp. nov.

A. platyceras Fedde, in Pflanzenr. 4 (104): 283. 1909, in small part; not *A. platyceras* L. & O.

Herba perennis latice pallide citreo, paene albido. Caules solitarii vel plures, 5-8 (-10) dm. alti, saepe decumbentes, diffuse ramosi omnino robuste et densius irregulariter aculeati, prope apices juvenales densissime aculeati. Folia profunde lobata fere usque ad costam, sinibus rectangularibus, lobis angustis saepe 5 vel plus longioribus quam latioribus, aliquando lobis brevibus secundariis, dentibus deltoideis, sparse aculeata subter in venis et supra in costa. Alabastra oblongo-elliptica, 12-15 mm. lata, 15-18 mm. longa, aculeata. Sepalorum cornua 12-15 mm. longa, tenua, aculeata. Flores 7-10 cm. diametro, petalis albis obovato-cuneatis, staminibus 100 vel plus, stigmate purpureo. Capsulae 3-carpellatae anguste elliptico-oblongae, 10-14 mm. latae spinis excludentibus, 35-45 mm. longae stylo tenui et stigmate includentibus, spinis tenuibus irregulari magnitudine 8-10 mm. longis armatae. Semina circa 2 mm. longa.

Perennial with pale lemon-yellow, almost white latex; stems 1-several, mostly 5-8 (-10) dm. tall, often decumbent, diffusely branched, closely prickly on the older parts with long, slender, uneven-sized, straight, perpendicular prickles, very densely prickly near the growing tips; basal and lower cauline leaves to about 20 cm. long, reduced upward, oblanceolate below to elliptic-lanceolate above, the blades deeply and distantly lobed to near the midrib, the sinuses rectangular, the lobes narrow, often five or more times as long as broad, sometimes with short secondary lobes, the primary and secondary lobes marginally toothed with deltoid teeth, each of which is terminated by a slender prickle, the under surfaces very sparingly prickly with long, rigid, straight prickles on the veins, the upper surfaces nearly smooth except for a few prickles on the midrib; buds elliptic-oblong, the body 12-15 mm. broad, 15-18 mm. long, armed with long, uneven-sized, simple prickles, the sepal horns extremely slender, terete, 12-15 mm. long including the long terminal spine, prickly on the basal one-half; flowers 7-10 cm. in diameter; petals white, obovate-obcuneate; stamens numerous, 100 or more, the filaments pale yellow, the anthers yellow; stigma purple, about 2-3 mm. broad, 2.0-2.5 mm. high, 3-lobed; capsules 3-carpellate, narrowly elliptic-oblong, the width, not including the armature, 10-14 mm., the length, including the slender style and stigma, 35-45 mm., closely beset with simple, slender, uneven-sized, straight spines, the largest of which may be 8-10 mm. long, the capsular surface clearly visible through the armature; seeds about 2 mm. long. (Ill.: Fig. 14, 1-4; Dist.: Fig. 18.)

Holotype: *Alice Eastwood & John T. Howell* 1003, from Grand Canyon National Park, "Kaibab trail to Roaring Springs," Arizona, June 23, 1933 (CAS; isotype, POM).

Habitat and distribution: Precipitous slopes of north wall of Grand Canyon along the Kaibab Trail, at elevations of possibly 3000-5000 ft., on unstable substratum; known only from the type locality.

Flowering and fruiting dates: Flowering begins in early June and may continue into October; fruits ripen from August until late autumn.

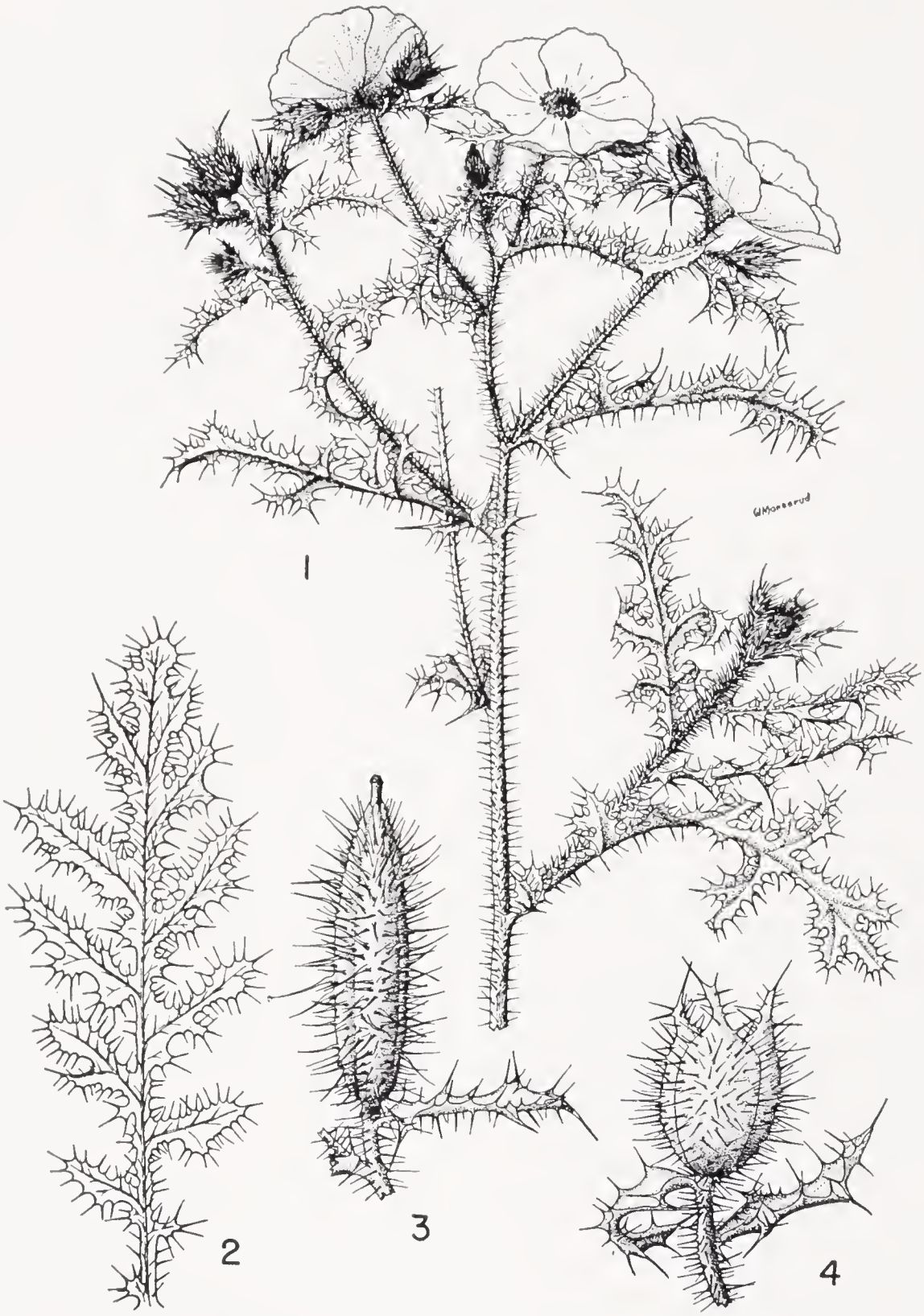

FIG. 14. *A. arizonica*. 1. Habit × ½. Holotype, *Eastwood & Howell* 1003 (CAS). 2. Leaf × ½. Topotype, *Ownbey & Ownbey* 1817 (MIN). 3. Capsule × 1. Liquid preserved material of topotype, *Ownbey & Ownbey* 1817 (MIN). 4. Bud × 1. Same as 3.

The distinguishing characteristics of this species are its deeply pinnatifid, remotely lobed leaves, its long and slender, uneven-sized prickles, its unusually long and slender sepal horns, its very pale lemon-yellow latex and its diffusely branching stem. Its affinities are uncertain, but possibly it is most closely related to *A. pleiacantha* subsp. *pleiacantha*. Two specimens seen by Fedde (US) were annotated and cited as *A. platyceras* L. & O., but this species as delimited in Fedde's monograph of the genus is composed of many irreconcilable elements.

First collected by F. H. Knowlton in 1889, *A. arizonica* has gone unrecognized until now. Due to the inaccessibility of much of the Grand Canyon its distribution within the canyon remains to be determined, but it is certainly comparatively localized.

Specimens examined: UNITED STATES.

ARIZONA

Grand Canyon National Park: Kaibab Trail to Roaring Springs, *Eastwood & Howell* 1003 (CAS, holotype of *A. arizonica* Ownb.; isotype, POM); Bright Angel Trail, Grand Canyon of the Colorado River, *Eastwood* 3679 (CAS); Kaibab Trail to Roaring Springs, *Eastwood & Howell* 7070 (CAS); Bright Angel Trail, alt. 4800 ft., *Goldman* 2221 (US); in the Grand Canyon of the Colorado, *Knowlton* 271 (US); Grand Canyon, alt. 2000-3000 ft., *McDougal* 240 (US); Kaibab Trail, about 3 miles from north terminus, *Ownbey & Ownbey* 1817 (ARIZ, CAS, COLO, F, GH, K, MIN, MO, NEW MEX, NY, POM, RM, SMU, TEX, UC, US).

14. ARGEMONE PLEIACANTHA Greene, in Fedde's Rep. Spec. Nov. 6: 161. 1908.

Annual or perennial with bright yellow or very pale lemon latex; stems 1-12 (-18) from the base, 5-12 dm. tall, mostly 10-20 mm. in diameter at the base, cymosely branched in the upper half, often purplish, sparingly to rather closely prickly throughout with ordinarily stoutish, rather even-sized, perpendicular prickles; leaves oblanceolate below, becoming elliptic-lanceolate upward, the upper ones sometimes clasping the stem, shallowly lobed to very deeply pinnatifid, the lamina surfaces sparingly armed principally on the veins beneath, smooth or more weakly prickly principally on the midrib above; buds subspherical or more often oblong-obovate, the body 11-18 (-22) mm. in diameter, 14-20 (-26) mm. long, sparsely to moderately prickly with simple or in part compound prickles, the sepal horns adaxially flattened and abaxially convex, or nearly terete, 4-12 mm. long including the apical spine; flowers 8-12 (-16) cm. in diameter; petals white; stamens about 150, the filaments pale yellow to red, the anthers yellow; stigma purple, 3-5 mm. broad, 2.5-4 mm. high, 3-4-lobed; capsules 3-4-carpellate, ovate to elliptic-lanceolate when mature, the width 10-16 (-18) mm., the length including the stigma 25-45 (-50) mm., densely spinescent to very sparsely spinescent, the longest spines 4-6 (-8) mm. long, these rarely with small secondary prickles near the base; seeds 2.0-2.5 mm. long.

Holotype: *O. B. Metcalfe* 1076, in dry gravel, approximate altitude, 6600 ft., Kingston, Sierra Co., New Mexico, July 6, 1904 (US; isotypes, CAS, F, GH, MIN, MO, NY, POM, UC, US).

Key to the subspecies:

1. Leaves usually deeply lobed; largest prickles of the buds often with secondary prickles; capsules usually closely spinescent; latex bright yellow when fresh; s.w.

New Mexico, s.e. Arizona and adjacent Chihuahua and Sonora . . . . . 14a. *A. pleiacantha* subsp. *pleiacantha*

1. Leaves very deeply to shallowly lobed; prickles of the buds all simple; capsules sparsely spinescent; latex pale lemon or bright yellow when fresh.
   2. Leaves pinnatifid to near the midrib, the sinuses rectangular, not at all clasping the stem at the base, latex very pale lemon; Sacramento Mts., New Mexico . . . . . 14b. *A. pleiacantha* subsp. *pinnatisecta*
   2. Leaves more shallowly lobed, sometimes manifestly clasping the stem at the base; latex bright yellow; central Arizona . . . . . 14c. *A. pleiacantha* subsp. *ambigua*

14a. Argemone pleiacantha Greene subsp. pleiacantha

A. pleiacantha Greene, in Fedde's Rep. Spec. Nov. 6: 161. 1908.

A. hispida Torrey, in Pac. R. Rep. 7 (3): 7. 1856; Hemsl., Biol. Cent. Am., Bot. 1: 27. 1879, as to Thurber's collection from Sonora; not *A. hispida* Gray.

A. platyceras var. *typica* Prain, in Journ. Bot. 33: 367. 1895, in small part; not *A. platyceras* L. & O.

A. platyceras var. *typica* Prain "state" β Prain, l.c., p. 368, in part; not *A. platyceras* L. & O.

A. munita Rose, in Contr. U. S. Nat. Herb. 8: 27. 1903; not *A. munita* Dur. & Hilg.

A. platyceras Fedde, in Pflanzenr. 4 (104): 283. 1909, in large part; Fedde, l.c., p. 274, fig. 36M, N, O; Woot. & Standl., Fl. N. Mex., in Contr. U. S. Nat. Herb. 19: 261. 1915, in part, as to New Mexico distribution; Kearn. & Peeb., Fl. Pl. Ariz., p. 336. 1942; Kearn. & Peeb., Ariz. Fl., p. 324. 1951, as to Arizona distribution; not *A. platyceras* L. & O.

A. platyceras var. *horridissima* Fedde, in Pflanzenr. 4 (104): 284. 1909, nomen nudum; not *A. platyceras* L. & O.

A. platyceras var. *pleiacantha* Fedde, l.c., p. 285; not *A. platyceras* L. & O.

A. platyceras var. *stenoceras* Fedde, l.c., p. 285; not *A. platyceras* L. & O.

Annual or perennial with bright yellow latex, often persisting by basal offshoots; stems 1-several from the base, 5-12 dm. tall, sparingly branched in the upper half, armed with scattered prickles to rather closely prickly, the prickles perpendicular; leaves oblanceolate to elliptic-lanceolate in outline, the cauline not manifestly clasping the stem, mostly deeply lobed, the broad sinuses reaching one-half to four-fifths the distance to the midrib, the lobes oblong, with marginal, deltoid teeth, each of which is terminated by a weak prickle, otherwise the leaves armed with scattered prickles on the veins, especially on the midrib beneath, often nearly smooth above; buds more or less closely subtended by the foliar bracts, but not obscured by them, the body subspherical to oblong-obovate, 12-18 (-22) mm. in diameter, 14-20 (-24) mm. long, sparsely to moderately prickly, often some of the larger prickles with one or more secondary prickles from the base, the sepal horns often adaxially flattened and abaxially convex, 8-12 (4-) mm. long, the horns conspicuously prickly and terminated by a basally flattened spine; flowers 8-12 (-16) cm. in diameter when fully open; petals white; stamens 150 or more, the filaments pale yellow to red, the anthers yellow; stigma purple, 3-5 mm. broad, 2.5-4.0 mm. high, 3-4-lobed; capsules 3-4-carpellate, ovate to elliptical when mature, the width, not including the armature, 10-16 mm., the length, including the stigma 30-45 (24-) mm., more or less closely spinescent with straight or incurved spines, the largest usually less than 6 mm. long, these rarely with small secondary prickles near the base, the capsular armature usually not completely obscuring the surface; seeds about 2 mm. long. (Ill.: Fig. 15, 3-6; Dist.: Fig. 18.)

Holotype: That of the species.

Habitat and distribution: Dry, gravelly, often disturbed soil, roadways, abandoned fields, and drainages, foothills and adjacent high plains, southwestern New Mexico, southeastern Arizona and adjacent Mexico, at elevations of 2500-7500 ft.

Flowering and fruiting dates: First flowers are produced in southern Arizona about April 1; flowering continues throughout the summer and fall until early November; late flowers often occur on new axillary shoots from the bases of the early stems; fruits begin to mature about June 15 and continue to mature until November.

The distinguishing characteristics of *A. pleiacantha* subsp. *pleiacantha* are the often deeply pinnatifid leaves which are only sparsely prickly on the main veins, the moderately prickly buds, the larger prickles of which often bear secondary prickles from the base, and the capsules which usually are densely prickly with uneven-sized prickles. The subspecies is easily separated from *A. hispida* with which it is sometimes confused by the absence of the crisped indumentum characteristic of the latter species. Its distribution is also completely disjunct from *A. hispida*. *A. pleiacantha* subsp. *pleiacantha* has often been lumped with *A. platyceras*, in the broad sense. *A. platyceras*, as delimited here, is a very distinct species differing from *A. pleiacantha* in many ways such as in its radially flattened sepal horns, its often pale lemon petals, its lower stamen number and its lack of compound prickles on the buds. Geographically, the two species are widely separated.

A. platyceras var. *horridissima* Fedde (in herb.; US) represents the most stoutly armed extreme of *A. pleiacantha* subsp. *pleicantha*. Plants of this sort are occasionally collected in New Mexico and Arizona. There may be sufficient basis for allowing this extreme phase the status of forma but, for the present, I believe it best not to recognize it nomenclatorially.

A. platyceras var. *stenoceras* is known only from the type specimen. It appears to be the smoothest phase of *A. pleiacantha* subsp. *pleiacantha*. The leaves partially clasp the stem at the base and are less deeply pinnatifid than is typical of the subspecies. The prickles of the buds are scattered and all are simple. The capsules appear to be typical of the subspecies although they are immature on the type specimen. For the present, at least, I feel that this proposed variety should be placed in synonomy.

Collections of *A. pleiacantha* subsp. *pleiacantha* from northwestern Chihuahua and northeastern Sonora are noteworthy for their less densely armored capsules. Such variations may be of significance but no inferences are possible at present.

Specimens of *A. pleiacantha* ssp. *pleiacantha* were cited by Prain in his revision of *Argemone* as part of *A. platyceras* var. *typica* "state" β. They comprised one of the larger elements of this heterogeneous group. In Fedde's revision, numerous specimens of this taxon were cited under *A. platyceras* proper, e.g., *Mearns* 59, *Wilcox* 101, *Toumey s.n.*, *Rose* 1299, and *Nelson* 6346.

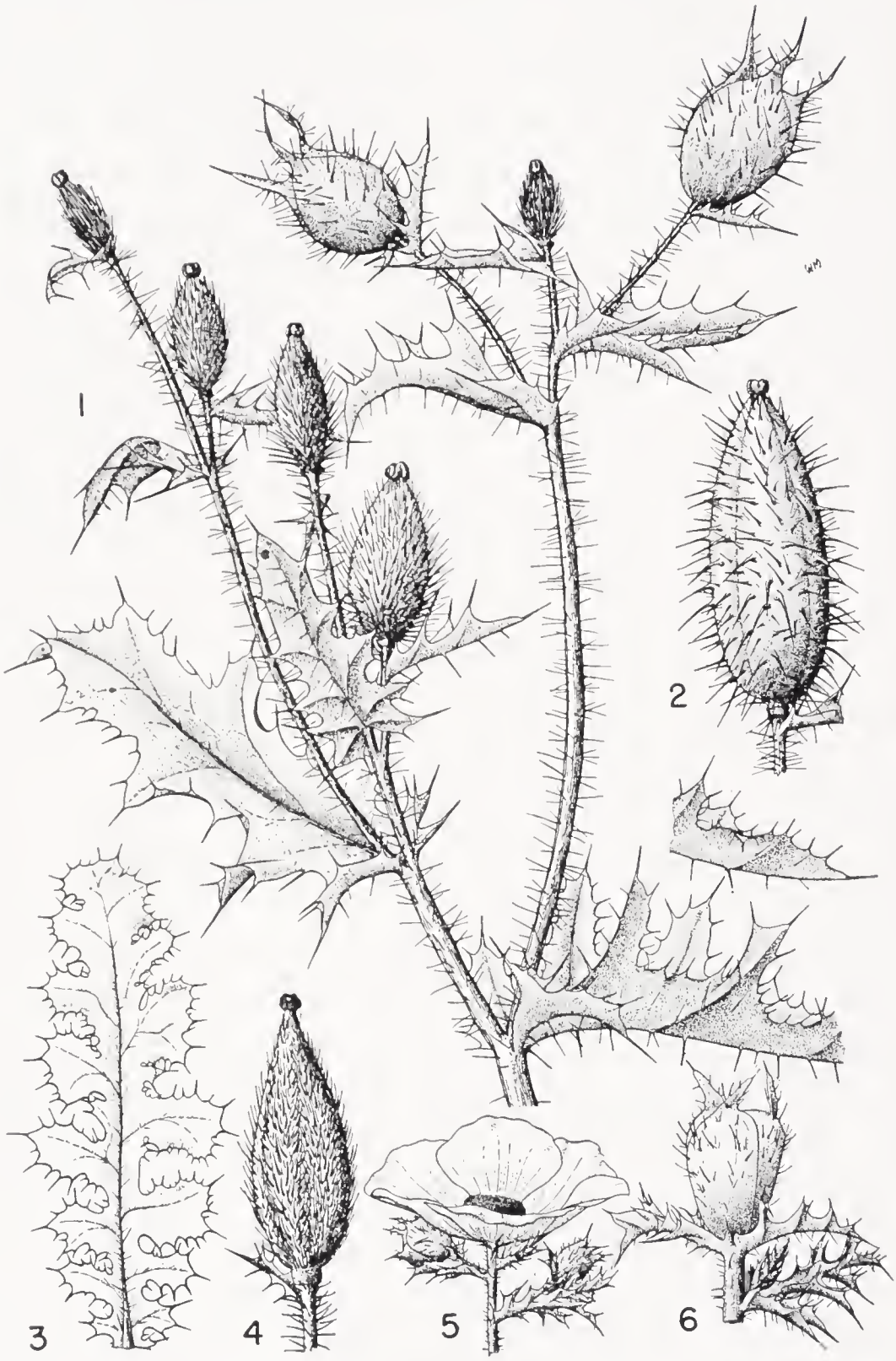

FIG. 15. 1-2. *A. pleiacantha* subsp. *ambigua*. 1. Habit × 1. Holotype, *Ownbey & Ownbey* 1827 (MIN). 2. Capsule × 1. Same as 1. 3-6. *A. pleiacantha* subsp. *pleiacantha*. 3. Upper surface of leaf × ½. Holotype, *Metcalfe* 1076 (US). 4. Capsule × 1. *Ownbey & Ownbey* 1474 (MIN). 5. Flower with buds × ½. Buds, *Ownbey & Ownbey* 1465; liquid preserved flowers of *Ownbey & Ownbey* 1757 (MIN). 6. Bud × 1. Liquid preserved material of *Ownbey & Ownbey* 1757 (MIN).

Putative natural hybrids between *A. pleiacantha* subsp. *pleiacantha* and *A. gracilenta* are sometimes found. The natural distribution of the former is in the foothills areas of southwestern New Mexico, southeastern Arizona and adjacent Chihuahua and Sonora. *A. gracilenta* is native to the flat valley floors and deserts of west-central Arizona southward in the Sonoran Desert for several hundred miles. The two species are fairly well separated ecologically and probably do not occur sympatrically except by introduction of *A. pleiacantha* into the irrigated valleys of the region especially along roadways and field borders. The existence of either species in these peripheral areas may be quite ephemeral and suitable conditions for direct interaction may not occur except at widely spaced and irregular intervals in time.

It is very difficult to assess the genetic effects of bringing these two species into proximity. Numerous examples of variation of a sort which would be attributed to hybridization could be enumerated. In the vicinity of Tucson, Arizona, both species and much aberrant material have been collected; much of the aberrant material is herein cited under *A. pleiacantha* subsp. *pleiacantha*. Some of these specimens have larger buds, larger capsules and larger leaves than is typical of the subspecies as found to the eastward. Some of them show characteristics of *A. gracilenta*, for example, *Toumey s.n.* (NY) has leaf margins and texture much as in *A. gracilenta; Thornber* 326 (US) has leaf margins, texture, capsule and bud enations intermediate between the two species; *Ownbey & Ownbey* 2095, collected near Cotaro, Ariz., is possibly a little closer in over-all aspect to *A. gracilenta* than to *A. pleiacantha*. At Magdalena, Sonora, some specimens, e.g., *Rose, Standley & Russell* 15115 (NY, US) exhibit the type of gigantism seen in the Tucson plants; *Rose, Standley & Russell* 15114 (US) is highly aberrant in leaf cuttings and enations of the capsules and buds.

Natural hybridization between *A. pleiacantha* subsp. *pleiacantha* and *A. ochroleuca* subsp. *ochroleuca* evidently is to be expected if the two occur together, a situation rarely met with in nature. *A. ochroleuca* occurs only as an introduced weed within the natural area of *A. pleiacantha*. Natural hybrids, probably all of the first generation, have been collected by my wife and myself at several localities in Sonora. The putative hybrids seen invariably occurred as isolated individuals, sometimes in the vicinity of one or both parents. No evidence of back-crossing was detected. The morphological appearance of the hybrids was normal in every respect and a large quantity of seeds was matured in each capsule.

Putative hybrids between *A. ochroleuca* and *A. pleiacantha* are large, vigorous plants with one or more stems from the base. The stems are often over a meter tall and the plants are conspicuous because of their large lemon-yellow flowers. In foliage characters they are distinctly intermediate

between the parents; likewise, the capsule armature is intermediate, consisting of intermixed coarse and fine spines of intermediate density. The stamen number is about 125, a number consistent with the expected result of crossing a species with a high stamen number with one having a low stamen number. Hybrid plants collected are as follows: *Ownbey & Ownbey* 1777c, from 27.9 miles s.w. of Moctezuma (GH, MIN); *Ownbey & Ownbey* 2078, from 3.6 miles n. of Imuris, Nogales-Magdalena road (MIN); *Ownbey & Ownbey* 2088, from 3.1 miles n.e. of Santa Ana on road to Magdalena (ARIZ, GH, MIN, US).

Specimens examined: UNITED STATES.

Arizona

Apache Co.: 3.1 miles n.w. of Eagar (Hwy. 73), *Ownbey & Ownbey* 1811 (ARIZ, BRY, COLO, F, ILL, MIN, NY, OKL, RSA, TEX, UC). Cochise Co.: Stephens' Ranch (Chiricahua Mts.), alt. 5700 ft., *Stephens s.n.* (*Blumer* 1814) (DS, GH, KSC, MIN, MO, NY, RM, US); Ft. Huachuca, *Wilcox* 101 (US). Navajo Co.: 11.4 miles s.w. of Show Low, *Ownbey & Ownbey* 1804 (ARIZ, BM, CAS, GH, MICH, MIN, NEW MEX, POM, RM, SMU, UTC, US); Taylor, *Zuck s.n.* (MO, NY, US). Pima Co.: Valley of the Rillito (Creek), *Pringle* 13616 (MO, PH, US); Tucson, *Toumey s.n.* (GH, NY, UC, US). Santa Cruz Co.: valley of Santa Cruz River, w. of Patagonia Mts., *Mearns & McVay* 1163 (NY); Calabasas, *Rose* 11945 (F, US); e. of Nogales, *Tidestrom* 765 (US). Yavapai Co.: 2.8 miles s.w. of Ashfork, *Ownbey & Ownbey* 1825 (ARIZ, CAS, GH, K, MICH, MIN, POM, UTC).

New Mexico

Catron Co.: Beaverhead, alt. 2100 m., *Eggleston* 20450 (MO); Mogollon Mts., *Saunders s.n.* (CAS). Grant Co.: Dog Spring (s.e. corner of the Co.), *Mearns* 59 (US, type collection of *A. platyceras* var. *horridissima* Fedde; isotype, DS); Mangas Springs, 18 miles n.w. of Silver City, alt. 4770 ft., *Metcalfe* 646 (MIN, MO, ND, NY, RM, UC, US); 12.7 miles s.e. of Hurley, *Ownbey & Ownbey* 1467 (MIN); 2.4 miles e. of Separ, alt. 4500 ft., *Ownbey & Ownbey* 1757 (ARIZ, BRY, DAO, GH, MICH, MIN, NEW MEX, POM, SMU, UC); Silver City, *Snow s.n.* (CANU, MIN, MO, US); Cliff, *Wooton s.n.* (US). Hidalgo Co.: Cloverdale, *Mearns* 519 (US); 27 miles s. of Animas, alt. 5000 ft., *Wolf* 2572A (CAS, DS, GH, RSA). Luna Co.: 11.4 miles e. of outskirts of Deming, *Ownbey & Ownbey* 1465 (ARIZ, COLO, MIN, NEW MEX, NY, RM). Sierra Co.: Kingston, alt. 6600 ft., *Metcalfe* 1076 (US, holotype of *A. pleiacantha* Greene; isotypes, CAS, F, GH, MIN, MO, NY, POM, UC, US); 2.2 miles w. of Kingston, *Ownbey & Ownbey* 1474 (BM, CAS, GH, K, MIN, UC, US); Chiz (near Winston), *Wooton* 2906 (NEW MEX, UC, US).

MEXICO.

Chihuahua

Sierra Madre w. of Pearson, *Barlow s.n.* (F); Casas Grandes, *Goldman* 416 (GH, US); St. (i.e., San) Diego, alt. 6000 ft., *Hartman* 673 (GH, US); between Colonia García and Pratt's Ranch below Pacheco, alt. 6000-7500 ft., *Nelson* 6273 (US, type collection of *A. platyceras* var. *stenoceras* Fedde); between Casas Grandes and Sabinal, alt. 5000-5500 ft., *Nelson* 6346 (US); 47.2 miles s.w. of Casas Grandes on road to García, *Ownbey & Ownbey* 2028 (GH, MIN, US); 16.2 miles s.w. of Casas Grandes on road to García, *Ownbey & Ownbey* 2031 (ARIZ, MICH, MIN, NY, RM, UC); 11.7

miles s.w. of Casas Grandes on road to García, *Ownbey & Ownbey* 2032 (BM, CAS, COLO, MIN); 10.1 miles s.w. of Casas Grandes on road to García, *Ownbey & Ownbey* 2033 (F, GH, K, MEXU, MICH, MIN, MO, POM); Carretas (Gran Morelos), border of Chihuahua and Sonora, alt. 4800 ft., *White* 2496 (GH, US).

SONORA

El Alamo, w. Magdalena, *Kennedy* 7064 (UC, US); 7.2 miles n. of Esqueda, *Ownbey & Ownbey* 1767 (ARIZ, GH, MICH, MIN, NY, RSA, UC, US); 0.7 mile n. of Esqueda, *Ownbey & Ownbey* 1768 (BM, CAS, COLO, F, MEXU, MIN, NEW MEX, POM, RM, TEX, WIS, WS); 27.9 miles s.w. of Moctezuma, *Ownbey & Ownbey* 1777b (ARIZ, GH, MIN, UC, US); 15.2 miles s. of Nogales, *Ownbey & Ownbey* 2077 (ARIZ, CAS, MEXU, MIN, NY, RM, RSA, UC, US); between Nogales and Guaymas, *Rose* 1299 (US); Magdalena, *Rose, Standley & Russell* 15114 (NY, US); Magdalena, *Rose, Standley & Russell* 15115 (NY, US); Colonia Oaxaca, *White* 420 (GH); Horocintos, Río Huachinera, region of the Río de Bavispe, *White* 2977 (GH, MEXU); 6 miles e. of Agua Prieta, alt. 3900 ft., *White* 3832 (GH); San José Mts., 2 miles s. of Naco, alt. 5000 ft., *Wolf* 2536 (CAS, DS, RSA).

14b. ARGEMONE PLEIACANTHA Greene subsp. **pinnatisecta** G. B. Ownb., subsp. nov.

A. platyceras Woot. & Standl., Fl. N. Mex., in Contr. U. S. Nat. Herb. 19: 261. 1915, in part, at to New Mexico distribution; not *A. platyceras* L. & O.

Herba annua aut perennis latice pallide citreo. Caules plerumque 3-12, 6-10 dm. alti, omnino robuste et regulariter aculeati. Folia usque ad et prope costam pinnatifida lobis distantibus, sinibus rectangularibus. Alabastra aculeis simplicibus. Sepalorum cornua subteretia. Capsulae 3-4-carpellatae, ellipticae vel late lanceolatae, aliquantum regulariter sed sparse spinescentes. Semina circa 2.5 mm. longa.

Annual or perennial with pale lemon, almost white latex; stems usually 3-12 from the base, 6-10 dm. tall, mostly 15-20 mm. in diameter at the base and retaining their diameter well upward, often purplish, cymosely branched in the upper half, stoutly and evenly prickly throughout, the prickles perpendicular; leaves oblanceolate, the lower cauline ones about 15 cm. long, progressively somewhat reduced in size upward, not clasping the stem, pinnatifid to near the midrib, the lobes distant, concave, with angular secondary lobes which are spine-tipped, the sinuses rectangular, the lamina surfaces sparingly and stoutly prickly on the under surfaces and veins, smooth above except for the midrib which has a few prickles; buds obovate, the body 12-14 mm. in diameter, 16-18 mm. long, moderately prickly, the simple prickles perpendicular, the sepal horns almost terete, 5-8 mm. long including the indurated apical spine; flowers 8.0-9.5 cm. in diameter; petals white, the outer margins undulate, the inner petals deltoid, the outer margin rounded, broadest just below the apex, about as broad as long, the outer suborbicular, broadest nearly one-half of the distance to the base; stamens about 150, with pale yellow filaments and yellow anthers, the inner filaments as long as the ovary at anthesis; stigma purple, about 3 mm. broad and high, 3-4-lobed; capsules 3-4-carpellate, elliptical, or slightly broader below the middle, when mature the width, not including the armature, 10-14 mm., the length, including the stigma, 25-40 mm., rather evenly but sparsely spinescent, the longest spines 4-5 mm. long, the capsular surface clearly visible; seeds about 2.5 mm. long. (Ill.: Fig. 16, 1-3; Dist.: Fig. 18.)

Holotype: *G. B. Ownbey & Findley* Ownbey 1754, from 9.6 miles west of Clouderoft, altitude 6600 ft., Otero Co., New Mexico, Aug. 12, 1953 (MIN; isotypes, ARIZ, BM, CAS, COLO, F, GH, MIN, NEW MEX, RM, RSA, UC, US).

Habitat and distribution: Gravelly hillsides and disturbed embank-

ments, evidently limestone soils, west slope of Sacramento Mts., New Mexico, at altitudes of about 6400-7200 feet, towards the upper limits of the pinon-juniper zone.

FIG. 16. *A. pleiacantha* subsp. *pinnatisecta*. 1. Habit × ½. Holotype, *Ownbey & Ownbey* 1754 (MIN). 2. Capsule × 1. Liquid preserved material of *Ownbey & Ownbey* 1753 (MIN). 3. Buds × 1. Same as 2.

Flowering and fruiting dates: Flowering begins about May 1 and continues through the summer; fruits mature from midsummer until autumn.

This subspecies differs from subsp. *pleiacantha* in its more sparingly prickly capsules, in its exclusively simple bud prickles, and in its very pale lemon yellow latex. The sinuses of the leaves are deeper and broader and the lobes correspondingly narrower and longer than is usual in other subspecies of *A. pleiacantha*. Distributionally, it is much restricted; no other *Argemone* has been recorded from its natural area.

Specimens examined: UNITED STATES.

New Mexico

Otero Co.: Sacramento Mts., *Earle* 585 (NY); 6.4 miles w. of Clouderoft, alt. about 7000 ft., *Ownbey & Ownbey* 1753 (BRY, ILL, K, MICH, MIN, MO, NY); 9.6 miles w. of Clouderoft, alt. 6600 ft., *Ownbey & Ownbey* 1754 (MIN, holotype of *A. pleiacantha* subsp. *pinnatisecta* Ownb.; isotypes, ARIZ, BM, CAS, COLO, F, GH, MIN, NEW MEX, RM, RSA, UC, UC); Rio Fresnal, Sacramento Mts., *Wooton s.n.* (US); La Luz Canyon, Sacramento Mts., *Wooton s.n.* (US).

14c. Argemone pleiacantha Greene subsp. **ambigua** G. B. Ownb., subsp. nov.

A. intermedia Kearn. & Peeb., Fl. Pl. Ariz., p. 336. 1942, in part; Kearn. & Peeb., Ariz. Fl., p. 324. 1951, in part, as to Arizona distribution; not *A. intermedia* Sweet.

Herba annua aut perennis latice flavo. Caules 1-8 (-18), 5-10 dm. alti, omnino distanter et sparse aculeati, aculeis subaequalibus. Folia leviter vel profundius lobata, superioribus saepe caulem amplectentibus. Alabastra subinermia vel moderate aculeata aculeis simplicibus. Sepalorum cornua plerumque ad axillas complanata, aliquando subteretia. Capsulae 3-4-carpellatae, plerumque elliptico-lanceolatae vel ovatae, aliquantum robuste et moderate vel levitissime et sparse spinescentes. Semina 2.0-2.5 mm. longa.

Annual or perennial with bright yellow latex; stems 1-8 (-18) from the base, about 5-10 dm. tall, mostly 10-16 mm. in diameter at the base, often purplish, cymosely branched from near the middle, distantly and sparingly prickly throughout with rather even-sized stoutish prickles on the main stem and weaker ones on the lateral, the prickles perpendicular; leaves to about 20 cm. long, reduced upward, oblanceolate below, lance-elliptic above, the upper cauline ones often clasping the stem, shallowly to rather deeply lobed, the lobes with angular secondary lobes which are prickly at the margins, sparingly and stoutly prickly on the veins beneath, sparingly prickly principally on the midrib above; buds obovate, the body 11-14 (-20) mm. in diameter, 14-18 (-26) mm. long, nearly smooth to moderately prickly with simple prickles, these perpendicular, the sepal horns sparingly prickly, usually flattened on the adaxial surface, sometimes nearly terete, 5-10 mm. long, including the apical spine; flowers 9-12 cm. in diameter; petals white, the inner deltoid, the outer deltoid-obovate; stamens about 150, with pale yellow filaments and yellow anthers, the filaments equalling or exceeding the ovary in length at anthesis; stigma purple, about 3-4 mm. broad and 2.5-3.0 mm. high, 3-4-lobed; capsules 3-4-carpellate, mostly elliptic-lanceolate or ovate, broader below the middle, when mature the width, not including the armature, 10-14 (-18) mm., the length, including the stigma, 26-36 (-50) mm., rather stoutly and moderately to very weakly and sparsely spinescent, the longest spines usually 4-6 (-8) mm. long, the capsular surface clearly visible; seeds 1.5-2.0 mm. broad, 2.0-2.5 mm. long. (Ill.: Fig. 15, 1-2; Dist.: Fig. 18.)

Holotype: *G. B. Ownbey & Findley Ownbey* 1827, from 10.3 miles n.e. of Prescott (Hwy. 89), Yavapai Co., Arizona, Sept. 10, 1953 (MIN; isotypes, ARIZ, CAS, COLO, F, GH, K, MICH, MIN, NEW MEX, NY, RM, RSA, UC, US).

Habitat and distribution: Slopes and meadows, roadways and embankments, well drained and usually gravelly soils, at altitudes of 3500-6000 ft., foothills of central Arizona.

Flowering and fruiting dates: Flowering begins about May 15 and continues until autumn; fruits begin to mature about July 1 and continue to ripen until November. Early flowering plants often flower again in the fall on lateral shoots, if moisture conditions permit.

This subspecies differs from subsp. *pleiacantha* in the very moderately to sparsely prickly capsules. The populations in the Ashfork and Prescott areas might almost be recognized as a separate subspecies. Plants from these areas have very large, elongate buds; the leaf sinuses often reach no more than one-half the distance to the midrib; the cauline leaf blades are comparatively broad at the base and more or less definitely clasp the stem. The need for further study of these populations is indicated. This subspecies together with *A. gracilenta* is probably the basis for the inclusion of *A. intermedia* (i.e. *A. polyanthemos*) in the Arizona Flora, by Kearney & Peebles. *A. polyanthemos*, according to my understanding of the species, does not occur within the state.

Evidence of hybridization between *A. pleiacantha* subsp. *ambigua* and *A. gracilenta* is found in some populations in west-central Arizona where their distributional areas impinge upon each other. Plants of putative hybrid origin combine the foliar and bud features of the parents. Those which vary in the direction of one or the other parent have been largely classified with the appropriate parent and cited thereunder. Putative hybrids of these two taxa are as follows: *Ownbey & Ownbey* 2166 from 4.1 miles n.e. of Valentine P. O., Mohave Co., alt. ca. 4000 ft. (ARIZ, CAS, GH, MIN, RM, RSA, UC, UTC, US); *Ownbey & Ownbey* 1826b, from 3.9 miles s. of Ashfork, Yavapai Co. (ARIZ, COLO, GH, MIN, RSA, UC, US).

Specimens examined: UNITED STATES.

ARIZONA

Coconino Co.: 0.8 mile e. of Flagstaff, *Ownbey & Ownbey* 1812 (ARIZ, GH, MIN). Gila Co.: Collom Camp, Matzatzal Mts., alt. 1200 m., *Collom s.n.*, 32 (GH, MO, ND, US); on road to Packard from Roosevelt, *Eastwood* 17136 (CAS); about 40 miles n.e. of Globe, alt. 4600 ft., *Kearney & Peebles* 12062 (CAS, POM); 16.6 miles s.e. of Roosevelt (Hwy. 88), *Ownbey & Ownbey* 1797 (ARIZ, COLO, MIN, NEW MEX, POM, RM, UC, US); 2.7 miles s.w. of Miami, *Ownbey & Ownbey* 1798 (BM, BRY, CAS, GH, MIN, NY, RSA, SMU, UTC); 37.2 miles n.e. of Globe (0.3 mile n.e. of Seneca), *Ownbey & Ownbey* 1803 (ARIZ, CAS, DAO, GH, MIN, NEW MEX, NY, POM, UC,

US, WS). Pinal Co.: Devil's Canyon near Superior, *Harrison* 2098 (US). Yavapai Co.: 2.2. miles e. of Ashfork, *Ownbey & Ownbey* 1824 (ARIZ, BM, BRY, CAS, COLO, F, GH, MIN, OKL, RM, RSA, UC, UTC, US); 10.3 miles n.e. of Prescott (Hwy. 89), *Ownbey & Ownbey* 1827 (MIN, holotype of *A. pleiacantha* subsp. *ambigua* Ownb.; isotypes, ARIZ, CAS, COLO, F, GH, K, MICH, MIN, NEW MEX, NY, RM, RSA, UC, US); 14.0 miles s.w. of Clarkdale, *Ownbey & Ownbey* 1828 (ARIZ, BM, BRY, ILL, MICH, MIN, POM, SMU, UTC, WIS, WS); western outskirts of Prescott, *Ownbey & Ownbey* 1829 (CAS, COLO, MIN, NY, RM); n. of Humboldt, *Tidestrom* 12713 (US); 2.9 miles n. of Rock Springs, *Ownbey & Ownbey* 2100 (ARIZ, GH, MIN, NEW MEX, UC, US); 1.6 miles s.w. of Peeples Valley, *Ownbey & Ownbey* 2105 (MIN).

15. Argemone platyceras Link & Otto, Ic. Pl. Rar. Hort. Berol., part 1: 85, t. 43. 1830 (1831?).

A. platyceras Otto & Dietr., in Allgem. Gartenzeit. 1: 300. 1833; Gray, Syn. Fl. N. Am. 1 (1): 88. 1895, in part; Rose, in Contr. U. S. Nat. Herb. 8: 26. 1903; Fedde, in Pflanzenr. 4 (104): 283, largely, excluding p. 274, fig. 36M, N, O.

A. platyceras var. *typica* Prain, in Journ. Bot. 33: 367. 1895, in part.

A. platyceras var. *typica* Prain "state" α Prain, l.c., p. 368.

A. mexicana var. *aculeatissima* Moric. ex Prain, l.c., p. 367, nomen nudum in synonomy; not *A. mexicana* L.

Annual or longer-lived, the latex color not known; stems 1-few, usually 3.0-7.5 dm. tall, sparingly branched near the top, weakly armed with scattered, straight, rather even-sized, perpendicular prickles; leaves bluish, the lower ones oblanceolate, the middle and upper ones elliptical to ovate, the uppermost often clasping the stem, lobed, the sinuses of the lower ones to two-thirds or more of the distance to the midrib, more shallowly lobed upward, the lobes oblong, marginally dentate, the teeth lanceolate to acute, each terminated by a weak prickle, the leaf surfaces sparingly prickly on the veins above and below with uniform prickles, to nearly smooth; buds oblong, the body 14-18 mm. broad, 18-24 mm. long, sparsely to moderately prickly, the sepal horns usually very distinctly flattened in a radial plane at least toward the tip when fresh, 6-9 mm. long, prickly to near the tip and terminated by a weak, indurated, flattened spine; flowers usually not closely subtended by the foliar bracts, 10-12 (-15) cm. broad when fully expanded; petals white or often faintly lemon-yellow when fresh, often obcuneate; stamens about 75, the filaments pale yellow to reddish-lavender, the anthers yellow to lavender; stigma 3-5 mm. broad, 2-3.5 mm. high, 4-5 lobed, the sterile tissue between the lobes usually visible; capsules 4-5-carpellate, broadly elliptical to elliptic-ovate, the body excluding the armature but including the stigma, 14-24 mm. broad, 25-45 mm. long, the surface more or less densely spinescent with simple, straight, slender spines, but less so on the sutures, the larger spines 6-8 mm. long, the armature sometimes nearly or completely obscuring the capsular surface; seeds about 2 mm. long. (Ill.: Fig. 17, 1-2; Dist.: Fig. 18.)

Type: It is uncertain if any of the original material was preserved. The illustration provided with the original description may be taken as the type. This is in accordance with the 1956 edition of the International Code of Botanical Nomenclature, Article 10. The type locality is "in Cofre de Perote Prope Hacienda de la Laguna," Vera Cruz, Mexico. See below for additional discussion.

Habitat and distribution: A very common weed, mostly in cultivated or abandoned fields, valley floors, precipitous slopes, often volcanic soils, highlands, Vera Cruz to southern Hidalgo, and the state of México; northwestern Michoacán; northern Oaxaca; at elevations of 6000 to 10,000 feet.

Flowering and fruiting dates; Not well defined. Flowers are produced throughout the year but probably most abundantly from April 15 onward through the summer months; ripe fruits are most abundant from about May 15 to November.

Rose, l.c., in discussing the origin of the original material of the species says: "The type of this species is said to grow 'in Cofre de Perote prope Hacienda de la Laguna.' Just what is meant by this statement is not clear. The 'Hacienda de la Laguna' is near Jalapa, Vera Cruz. A more accurate statement would probably be 'above Hacienda de la Laguna toward the Cofre de Perote.' Mr. Pringle and the writer collected on the mountains above Jalapa, and consequently near the type locality, a plant which seems to answer in all essential particulars to Link and Otto's figure."

The preferred name for the Cofre de Perote is now the Cerro Nauhcampatepetl according to the American Geographical Society 1:1,000,000 Map of Hispanic America, Sheet N.E-14, 1952. The straight line distance from Jalapa to the summit of the Cerro is about 15 miles. In terms of miles, then, the type locality as originally stated is not too incorrect, and Rose and Pringle were certainly near this locality when they collected in the mountains above Jalapa.

According to Prain (1895, p. 371), *A. platyceras* was introduced into European gardens in 1827. However, Link & Otto state that seeds were sent by Schiede and Deppe in 1829 and that plants flowered in Berlin in 1829 and 1830. The original description and illustration was drawn from these plants. I have seen no specimens of the original material of *A. platyceras* and have seen no reference to any in literature. It is doubtful if any was preserved, since Fedde would surely have cited specimens on deposit at Berlin at the time of his monograph.

The Gray Herbarium of Harvard University has most kindly reproduced the original diagnosis and illustrations of *A. platyceras* from their copy of the Icones for my use. The diagnosis is very lucid and the illustration highly accurate in all important details. There can be no question as to the identity of this species, even in the absence of preserved specimens of the original cultivated materials.

A. platyceras is most clearly differentiated by its weakly and sparingly armed leaves and stems, by its very characteristically flattened sepal horns, and by its usually densely prickly capsules. It is perhaps most closely allied to *A. pleiacantha* on grounds of comparative morphology. I do not believe this alliance to be close.

A. platyceras usually has been combined with other more or less related species native to northern Mexico and southwestern United States during the past sixty years. For example, *A. platyceras*, in the broad sense, as treated in Prain's monograph includes elements of true *A. platyceras* L.

& O., *A. hispida* Gray, *A. arida* Rose, *A. munita* Dur. & Hilg., *A. squarrosa* Greene, *A. pleiacantha* Greene, *A. sanguinea* Greene, *A. aurantiaca* Ownbey and *A. echinata* Ownbey. Only Prain's *A. platyceras* var. *typica* "state" α is true *A. platyceras* L. & O. His "state" β included elements of *A. arida, A. munita, A. pleiacantha, A. sanguinea* and *A. echinata;* his "state" γ is entirely *A. sanguinea;* his "state" δ is mostly *A. aurantiaca,* but in small part is *A. squarrosa. A. platyceras* var. *hispida* of Prain's monograph is largely *A. hispida* Gray but includes elements of *A. munita* subsp. *munita* and of *A. munita* subsp. *rotundata.* A. *platyceras* var. *chilensis* of the same author is a distinct species native to South America, *A. rosea* Hook.

In Fedde's treatment of *Argemone,* cited specimens of *A. platyceras* proper include specimens which are correctly placed here, e.g., *Kerber* 225a, *Pringle* 8967, 11369, *Rose & Hay* 5306, 5355, *Rose & Hough* 4288, 4730, etc. Fedde also cites numerous specimens under *A. platyceras* which belong to other species, viz., to *A. munita* subspp., *A. pleiacantha* subsp. *pleiacantha, A. squarrosa* subspp. *squarrosa* and *glabrata, A. sanguinea, A. polyanthemos, A. albiflora* subsp. *texana, A. aenea, A. arizonica* and *A. echinata,* and doubtless others. Several of these taxa are newly described in this paper, and Fedde was merely following the custom of his day in drawing the specific lines of *A. platyceras* sufficiently broad to include such a wide array of forms. In addition to *A. platyceras* proper, Fedde lists six varieties: Var. *gracilenta* is, I believe, a distinct species; var. *stenoceras* is, I believe, assignable to *A. pleiacantha* subsp. *pleiacantha;* var. *pleiacantha* is Greene's *A. pleiacantha* and is herein treated as *A. pleiacantha* subsp. *pleiacantha;* var. *hispida* is true *A. hispida* when from the Rocky Mts., is *A. munita* subspp. when from the Great Basin and adjoining areas, and is *A. echinata* as to *Pringle* 8294 from the Rio Grande Valley; var. *hispido-rosea* and var. *hunnemannii* are Chilean taxa not considered in this paper, but they certainly are not assignable to *A. platyceras* L. & O.

It is clear from the above summary that both Prain's and Fedde's treatments of *A. platyceras* included a multitude of forms under this binomial. It is now evident that this name should be applied in the original sense of Link & Otto, and that the anomalous elements included thereunder by Prain and Fedde should be assigned to other species.

Rose, whose understanding of Mexican argemones surpassed that of any of his contemporaries, definitely and correctly allowed *A. platyceras* L. & O. to stand in its original circumscription with the statement: "A. *platyceras* is certainly to be kept distinct from our United States and northern Mexican forms." The present writer, having studied this species

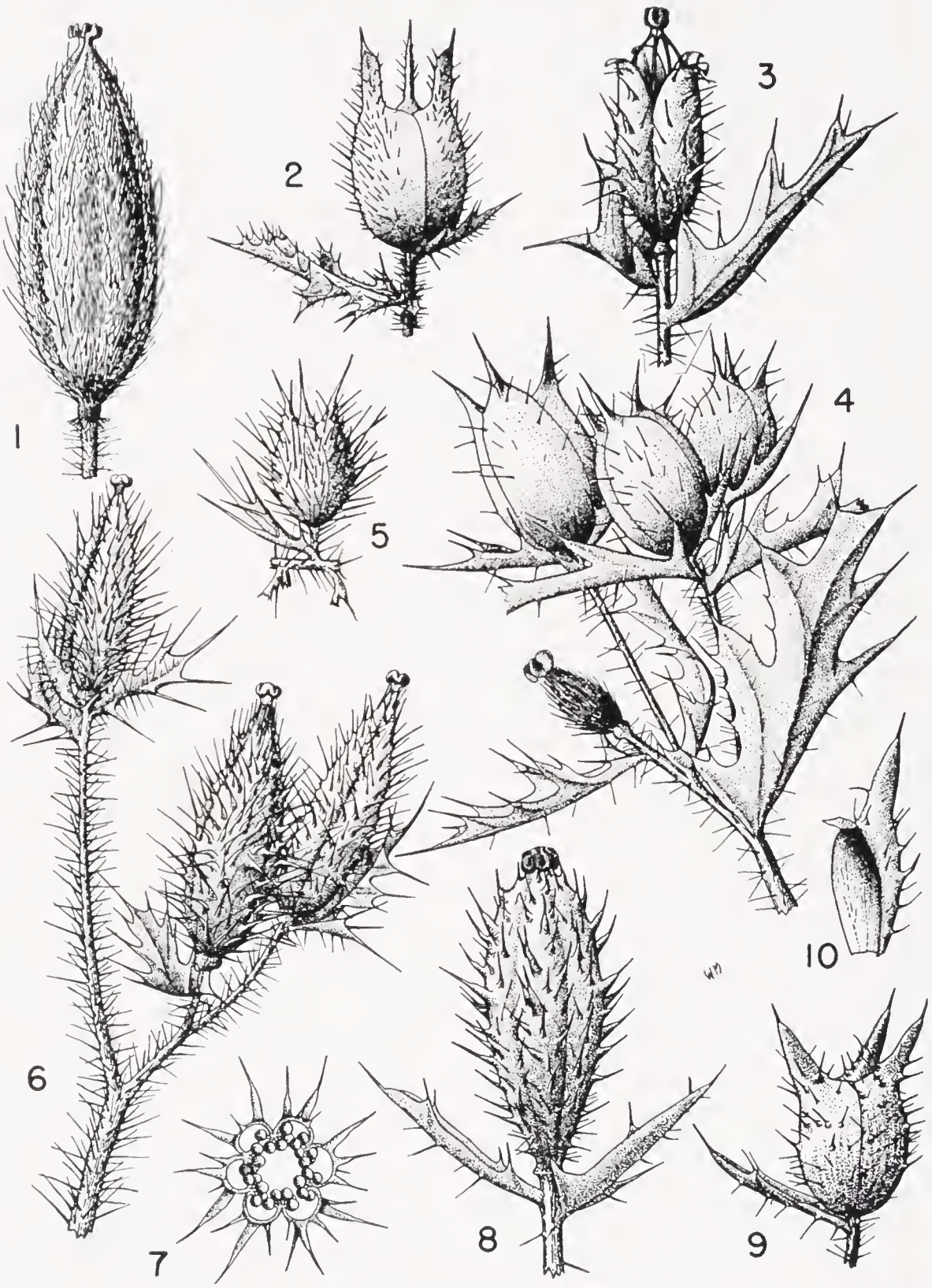

FIG. 17. 1-2. *A. platyceras.* 1. Capsule × 1. *Pringle* 11369 (US). 2. Bud × 1. *Balls* B4668 (UC). 3-4. *A. arida.* 3. Capsule × 1. *Ownbey & Ownbey* 1441 (MIN). 4. Habit × 1. Same as 3. 5-6. *A. chisosensis.* 5. Bud × 1. Isotype, *Ferris & Duncan* 3003 (CAS). 6. Capsules × 1. Holotype, *Ferris & Duncan* 3003 (NY). 7-10. *A. sanguinea.* 7. Capsule, x-section × 1. Liquid preserved material of *Ownbey & Ownbey* 1610 (MIN). 8. Capsule × 1. Same as 7. 9. Bud × 1. Same as 7. 10. Sepal × 1. Same as 7.

and all of the others mentioned above in the field, in the herbarium, and in large part under cultivation, concurs in this opinion.

Specimens examined: MEXICO.

FEDERAL DISTRICT

San Angel près Mexico, *Bourgeau* 7 (GH, UC, US); near Mixcoac, alt. 7500 ft., *Pringle* 8967 (CAS, F, GH, MEXU, MIN, MO, NY, UC, US); about Ajusco Station, alt. 9500 ft., *Pringle* 11369 (F, GH, MEXU, US).

MÉXICO

Real del Monte, *Herrera s.n.* (MEXU); Apam, *Millspaugh s.n.* (F); 9.7 miles n.w. of Colonia, *Ownbey & Ownbey* 1423 (F, GH, MIN, NY, US); between Pachuca & Real del Monte, *Rose, Painter & Rose* 8721 (GH, NY, US).

MÉXICO

Amecameca, alt. 8500 ft., *Balls* B4150 (UC); Ixtlahuaca, *Gregg* 720 (MO); Crucero Agua Blanca, *Hinton et al.* 6575 (F, GH, MEXU, NY, US); Amecameca, alt. 8600 ft., *Kuntze* 23651, *in part* (NY); 18.5 miles e. of Toluca, Hwy. 4, *Ownbey & Ownbey* 1429 (BM, CAS, F, GH, MEXU, MIN, NY, POM); 30.9 miles n.w. of Toluca (1.7 miles w. of Villa Victoria), *Ownbey & Ownbey* 2052 (COLO, K, MEXU, MIN, NY, RM, UC, US); near Ozumba, *Rose & Hay* 5355 (MEXU, US); near Toluca, alt. ca. 3000 m., *Schery* 81 (MO); S. Juan de Xico, Dist. de Chalco, ex herb. *Urbina s.n.* (MEXU).

MICHOACÁN

Cerro Tancítaro, Tancítaro, alt. 5000-9000 ft., *Leavenworth* 705 (F, GH); 17.0 miles w. of Zacapu, Hwy. 4, *Ownbey & Ownbey* 1432 (MIN); 1 mile e. of Carapán, *Ownbey & Ownbey* 1434 (GH, MICH, MIN, UC).

OAXACA

Valle de Nochixtlán, alt. 2180 m., *Conzatti* 4286 (MEXU, US); vicinity of Coixtlahuaca, alt. 7000-7500 ft., *Nelson* 1930 (US).

PUEBLA

Vicinity of Puebla, alt. 2150 m., *Arsène* 1299 (MO, US); Chalchicomula, *Smith* 113 (MIN, MO, US).

TLAXCALA

Santa Ana, alt. 2000 m., *Conzatti* 932 (GH).

VERA CRUZ

Above Los Molinos, Perote, alt. 9300 ft., *Balls* B4668 (UC); Orizaba, *Botteri* 261 (GH); Maltrata, *Kerber* 225a (CAS); Huatusco, *Mohr s.n.* (US); Las Vegas, *Rose & Hough* 4288 (US).

STATE UNKNOWN

Plantae Novae Hispaniae, *Sessé, Monciño, Castillo & Maldonado* 2261 (F).

16. ARGEMONE ARIDA Rose, in Contr. U. S. Nat. Herb. 8: 26. 1903.

A. platyceras var. *typica* Prain, in Journ. Bot. 33: 367. 1895, in small part; not *A. platyceras* L. & O.

A. platyceras var. *typica* Prain "state" β Prain, l.c., p. 368, in small part; not *A. platyceras* L. & O.

A. intermedia Fedde, in Pflanzenr. 4 (104): 281. 1909, in small part; not *A. intermedia* Sweet.

Annual or short-lived perennial with yellow to orange latex; stems 1-few, 3-7 (-10) dm. tall, branched in the upper portions, very moderately to rather copiously prickly throughout with perpendicular or slightly recurved, slender prickles; leaves glaucous, the lower ones lobed one-half to three-fourths the distance to the midrib, the upper ones sometimes more shallowly lobed, the lobes oblong, often longitudinally folded, the marginal teeth acute, the lower surfaces of the leaves moderately prickly on the veins, the upper surfaces smooth or sparingly prickly on the main veins; buds oblong, the body 12-15 mm. broad, 16-20 (-24) mm. long, sparingly and evenly prickly with ascending prickles, the sepal horns slender, sometimes flattened, the length 7-10 (-12) mm., often with a few prickles near the base, terminated by a weak spine; flowers 7-10 (-12) cm. broad, more or less closely subtended by 1-2 foliar bracts; petals white or with a faint lemon-yellow tinge, obcuneate, the outer more broadly so; stamens 80-120 or more, the filaments pale lemon-yellow to red, the anthers yellow or tinged with purple, the stamens and ovary subequal at anthesis; stigma 3-5-lobed, purple, about 3-4 mm. wide and 1.5-2.5 mm. high; capsules 3-5-carpellate, elliptic-oblong to lanceolate, the width, exclusive of armature, 12-15 mm., the length, including the stigma 25-40 (-45) mm., thinly to rather closely armed with uneven-sized spines and prickles, the largest spines to about 8 mm. long, the capsular surface sometimes partially obscured; seeds about 1.8-2.2 mm. long. (Ill.: Fig. 17, 3-4; Dist.: Fig. 18.)

Holotype: *J. N. Rose & Walter Hough* 4864 collected "on the arid plains about San Luis Potosí," San Luis Potosí, Mexico, July 13, 1899 (US).

Habitat and distribution: High prairies and intermountain plains, gravelly or alluvial soil, often a weed around corn and bean fields or other cultivated or disturbed areas, southern Chihuahua to San Luis Potosí, Mexico, at elevations generally between 5800 and 6800 feet.

Flowering and fruiting dates: Flowering probably begins about June 1 and continues through the summer and autumn at least through October; fruits are matured from July to November and December.

Argemone arida is one of the least known species of the genus because of the near absence of specimens in herbaria. It is most easily recognized by its oblong buds, slender sepal horns, obcuneate white or very pale lemon-yellow petals, usually red filaments and usually rather densely and simply spinescent capsules. On the basis of field observations, I am convinced that this species is most closely related to *A. platyceras*. It differs most markedly from *A. platyceras* in its less densely spinescent capsules and in its slender sepal horns which are usually quite unlike those of the latter species.

In the original description of *A. arida*, Rose mentions the long styles of the new species as of importance. The mature capsules of the holotype do have styles 2-4 mm. long, but in all other specimens of *A. arida* seen by the writer the style is 1 mm. or less in length. The holotype, therefore, is aberrant in this character and possibly even abnormal. Generally speaking, style length in *Argemone* has proved to be of little or no diagnostic value.

The only species of *Argemone* which occurs in the same distributional

area as *A. arida* is *A. ochroleuca*. These two species often occur side by side but evidently do not cross in nature.

Specimens examined: MEXICO.

CHIHUAHUA

14.4 miles e. of Hidalgo del Parral, *Ownbey & Ownbey* 1458 (MIN).

DURANGO

Ramos to Indé, *Nelson* 4719 (GH, US); 1.6 miles s.e. of Nombre de Dios, *Ownbey & Ownbey* 1444 (MIN); 6.3 miles n.e. of Villa Madero, *Ownbey & Ownbey* 1447 (MIN, US, UC); 8.6 miles n.w. of La Zarca, *Ownbey & Ownbey* 1453 (CAS, MIN, MO, NY); 26.9 miles s.e. of La Zarca on road to Durango, *Ownbey & Ownbey* 2034 (COLO, F, K, MEXU, MICH, MIN, RM, RSA, UC).

SAN LUIS POTOSÍ

Border of Jalisco, 10.6 miles e. of Ojuelos de Jalisco, *Ownbey & Ownbey* 2039 (ARIZ, CAS, COLO, F, GH, K, MEXU, MICH, MIN, MO, NY, RM, RSA, SMU, TEX, UC, US); 0.1 mile s.w. of San Luis Potosí, *Ownbey & Ownbey* 2040 (GH, MEXU, MIN, NY, US); 3.4 miles n.e. of Soledad Díez Gutiérrez, *Ownbey & Ownbey* 2041 (CAS, F, MIN, POM, UC); San Luis Potosí, *Rose & Hough* 4864 (US, holotype of *A. arida* Rose).

ZACATECAS

19.7 miles n. of Rincón de Ramos, *Ownbey & Ownbey* 1438 (K, MEXU, MICH, MIN, UC, US); 19.5 miles s.e. of Fresnillo, *Ownbey & Ownbey* 1441 (GH, MIN, MO); 4.2 miles n.w. of Sain Alto road junction with main hwy., *Ownbey & Ownbey* 2008 (CAS, COLO, F, MIN, MO); 4.9 miles s.e. of Zacatecas, *Ownbey & Ownbey* 2009 (MIN, NY, RM, RSA, SMU); 41.3 miles e. of Sombrerete on road to Fresnillo, *Ownbey & Ownbey* 2036 (GH, K, MEXU, MICH, MIN, NY, UC, US); 5.6 miles s. of Ojocaliente, *Ownbey & Ownbey* 2037 (C, CAS, F, GA, GH, K, MEXU, MIN, NY, RM, SMU, TEX, UC, US).

17. ARGEMONE SANGUINEA Greene, in Pittonia 4: 68. 1899.

A. sanguinea Rose, in Contr. U. S. Nat. Herb. 8: 25. 1903.

A. platyceras Wats., in Proc. Am. Acad. 17: 318. 1882, as to *Palmer* 20; Hemsl., Biol. Cent. Am., Bot. 4: 4. 1886, as to *Palmer* 20; Coult., in Contr. U. S. Nat. Herb. 2: 12. 1891, in part, excluding *A. hispida* Gray, in synonymy; Gray, Syn. Fl. N. Am. 1 (1): 88. 1895, in part; Small, Fl. s.e. U. S., p. 462. 1903, as to Texas distribution, in part; Fedde, in Pflanzenr. 4 (104): 283. 1909, in small part; not *A. platyceras* L. & O.

A. mexicana Britton & Rusby, in Trans. N. Y. Acad. Sci. 7:7. 1887; not *A. mexicana* L.

A. platyceras var. *rosea* Coulter, in Contr. U. S. Nat. Herb. 1: 30. 1890; Coult., l.c., 2: 12. 1891; Swift, in Addisonia 20: 49, t. 665. 1939; not *A. platyceras* L. & O.; not *A. rosea* Hook.

A. intermedia var. *typica* Prain, in Journ. Bot. 33: 363. 1895, in part; not *A. intermedia* Sweet.

A. platyceras var. *typica* Prain, l.c., p. 367, in small part; not *A. platyceras* L. & O.

A. platyceras var. *typica* Prain "state" β Prain, l.c., p. 368, in part; not *A. platyceras* L. & O.

A. platyceras var. *typica* Prain "state" γ Prain, l.c., p. 369; not *A. platyceras* L. & O.

A. mexicana var. *rosea* Coulter ex Greene, in Pittonia 4: 68. 1899, erroneous reference to *A. platyceras* var. *rosea* Coulter; not *A. mexicana* L.; not *A. rosea* Hook.

A. purpurea Rose ex Pringle, Pl. Mex., no. 8277. 1900, nomen nudum; Rose ex Fedde, in Pflanzenr. 4 (104): 280. 1909.

A. pinnatifida Norton, in Trans. Acad. Sci. St. Louis 12: 38. 1902.

A. delicatula Small (?), Fl. s.e. U. S., p. 462. 1903.

A. intermedia Fedde, in Pflanzenr. 4 (104): 281. 1909, in part; not *A. intermedia* Sweet.

A. pinnatifida f. *rosea* Cockerell, in Journ. N. Y. Entomol. Soc. 25: 192. 1917; not *A. rosea* Hook.

Annual, biennial or short-lived perennial with pale to bright yellow latex; stems 1-few, often 4-8 (-12) dm. tall, simple below, widely branched above, sparingly prickly with perpendicular to recurved prickles; leaves glaucous, the veins conspicuously light blue-lined, the lower cauline and basal deeply lobed to four-fifths the distance to the midrib, the middle and upper cauline often less deeply lobed, the lobes oblong and with marginal acute, prickle-tipped teeth, the lower surfaces moderately prickly on the main veins, the upper surfaces almost smooth to sparsely prickly on the main veins; buds broadly elliptic-oblong, the body 10-15 mm. broad, 12-20 mm. long, moderately prickly with spreading prickles, the sepal horns basally slightly prickly, often angular in cross-section, 5-10 mm. long including the indurated, sometimes slightly flattened apical spine; flowers 6-9 cm. in diameter, usually closely subtended by 1-2 small foliar bracts; petals white to lavender, broadly obovate-obcuneate to sub-orbicular, distally erose; stamens 150 or more, about equalling the ovary in length at anthesis, the filaments lemon yellow to red, the anthers yellow to lavender; stigma purple, not sinuate, about 2.5-5.0 mm. wide and 1.5-3.0 mm. high; capsules 3-5 (-6)-carpellate, narrowly to broadly elliptical, the width, exclusive of spines, 8-15 (-18) mm., the length, including the stigma, 25-40 (-50) mm., armed with stout, often recurved spines interspersed with smaller spines and prickles, the largest spines commonly 5-7 (-10) mm. long, the capsular surface clearly visible; seeds strongly apiculate at the micropyle, the longest dimension about 1.5 mm. excluding the micropylar beak. (Ill.: Fig. 17, 7-10; Dist.: Fig. 18.)

Holotype: *G. C. Nealley* 9, from Corpus Christi, Nueces Co., Texas, 1889 (F), i.e., the type of *A. platyceras* var. *rosea* Coulter. The number *9* is the serial number assigned to this taxon by Coulter in his publication, l.c.

Habitat and distribution: Roadways, field margins, embankments, vacant lots and generally disturbed areas; occasional in chaparral plains, sandy soils or evidently sometimes in limestone soils in the west; southern Texas and adjacent Mexico westward to Val Verde Co., but rare in western Texas; also in southern Coahuila; found at altitudes of near sea level in the east to 4000-5000 ft. in the west and south.

Flowering and fruiting dates: Most abundant flowering begins in late February and continues through March and April; fruits are ripened from late March through May, where conditions for growth are suitable in the essentially frost free parts of southern Texas and adjacent Mexico; however, flowers and fruits may be produced at any time during the year.

A. sanguinea is recognized by its deeply cut, conspicuosly light blue-lined leaves, its large white to lavender flowers, its elliptic-oblong buds which are rather sparingly prickly with spreading prickles, its usually long sepal horns and its elliptical capsules which are armed with uneven-

sized spines. The species is magnificently illustrated by Sorensen in Swift's account of the species under the name *A. platyceras rosea*. The distribution of *A. sanguinea* impinges upon that of *A. albiflora* subsp. *texana* to the north and immature specimens of the two taxa are sometimes difficult to distinguish. Ways of separating the two are discussed under the latter taxon.

The oldest name proposed for this species is *A. platyceras* var. *rosea* Coulter. This taxon is, however, specifically distinct from *A. platyceras* L. & O. Since the varietal name could not be raised to species rank because of the older *A. rosea* Hook., Greene rightly proposed a new name, *A. sanguinea*. Although Greene erroneously cited the original name as "*A. Mexicana*, var. *rosea*, Coulter, Bot. West Texas, p. 12," there can be no question as to his real intent and the new name must stand.

A. sanguinea is identical to "state" γ of *A. platyceras* var. *typica* Prain and, in part, is "state" β of the same author. It is only one of many diverse elements included under the variety by this author, and in actuality is not at all closely related to *A. platyceras*. Specimens of *A. sanguinea* are also cited by Prain under *A. intermedia* var. *typica*. Specimens of *A. sanguinea*, viz., *Nealley* 22 and *Heller* 1378, are cited under *A. platyceras* proper by Fedde.

A. pinnatifida Norton must be rejected because of Greene's earlier binomial. It refers, without question, to the same entity as *A. sanguinea*.

A. purpurea Rose was originally published by Pringle as a nomen nudum in a list of plants which he had collected. The collection cited was *Pringle* 8277 from near Eagle Pass, Texas. Many duplicates of this number, bearing the label name *A. purpurea* Rose, were distributed to herbaria. It must be assumed that Rose had proposed this name provisionally but that he realized that the taxon was conspecific with *A. sanguinea* before publication. It is notable that, in Rose's paper on the argemones of Mexico, *Pringle* 8277 is cited under *A. sanguinea*. Without regard for its debatable standing, *A. purpurea* Rose was validly published by Fedde. *Pringle* 8277 is the only specimen cited. The confusion is further increased in Fedde's revision when *A. sanguinea* Greene is placed in synonymy under *A. platyceras* as was done by Prain.

A. delicatula Small is of uncertain identity since no specimens were cited in the original description. Likewise, no authentic specimens bearing this label name have been found in herbaria. The name was omitted entirely in Small's manual. It seems most likely, however, that this name is most properly relegated to synonymy under *A. sanguinea*.

The treatment of *A. sanguinea* presented here must be considered preliminary. Morphologically, a great deal of variation is included under

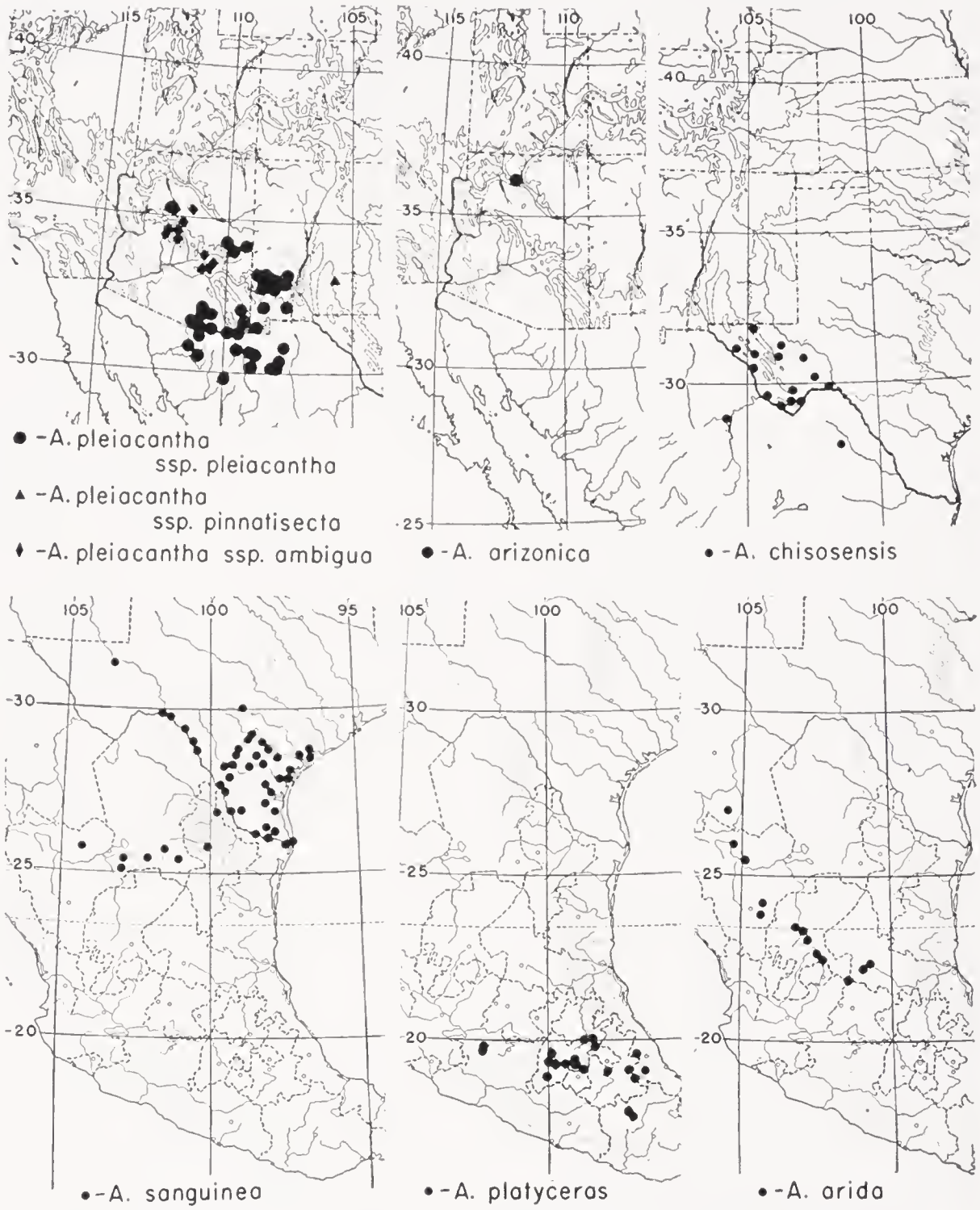

FIG. 18. Geographical distributions of species and subspecies as indicated.

this binomial. Whether or not several taxa are involved in producing this complex variation pattern probably cannot be demonstrated by descriptive methods although statistically significant differences between certain populations could probably be demonstrated. Extensive cytogenetic analysis of this and other Texas species is needed before any conclusions as to the biological nature of *A. sanguinea* can be drawn.

With regard to the Texas material, I am unable consistently to distinguish the diploid from the tetraploid phase of *A. sanguinea* on the basis of herbarium material. Many specimens have been collected only in early flower or in flower and very immature fruit and are of little value. Garden cultures of the two appear to be distinguishable as follows: The diploid phase has narrowly elliptical capsules which are more finely and densely prickly, very prickly buds and finely divided leaves; the tetraploid phase has broadly elliptical capsules which are less densely prickly, moderately prickly buds and more coarsely divided leaves. The diploid, on the basis of the limited data now available, appears to be absent from the eastern portion of the species range where the tetraploid is commonest.

Specimens examined: UNITED STATES.

TEXAS

Aransas Co.: near Rockport, *Whitehouse* 11807 (SMU). Atascosa Co.: 3 miles n. of Campbellton, *Whitehouse* 18396 (SMU). Bee Co.: 5.3 miles s.w. of Berclair, *Ownbey & Ownbey* 1604 (MIN). Bexar Co.: San Antonio, *Mackensen* 151 (F). Brooks Co.: Falfurrias, *Ownbey & Ownbey* 1613 (ARIZ, COLO, F, GA, GH, KSC, MICH, MIN, NY, SMU, TEX, UC, US, WIS, WS). Calhoun Co.: Port Lavaca, *Tharp* 1589 (TEX, US). Cameron Co.: 4.9 miles e. of Edcough, *Ownbey & Ownbey* 1617 (GH, MIN, UC, US). Dimmit Co.: Carrizo Springs, *Jones* 28235 (CAS, DS, MO, POM, RM, UC). Duval Co.: San Diego, *Croft* 98 (MIN, NY); San Diego, *Nealley* 22 (F, TEX, US). Frio Co.: Moore, *Eggert s.n.* (MO). Gillespie Co.: Crab Apple Cr., *Jermy* 218 (MO, US, duplicates of syntype of *A. pinnatifida* Norton). Goliad Co.: 3.9 miles n.e. of Goliad, *Ownbey & Ownbey* 1600 (MIN). Hidalgo Co.: 3.2 miles w. of Mission, *Ownbey & Ownbey* 1625 (BM, CAS, COLO, GH, ILL, MIN, NEW MEX, NY, UC). Jim Hogg Co.: between Guerra and Randado, *Tharp, Johnson & Webster* 48-28 (TEX). Jim Wells Co.: 1.9 miles n.e. of Alice, *Ownbey & Ownbey* 1609 (BM, CAS, F, MIN, NY, OKL, POM, RM, SMU). Karnes Co.: s. of Kenedy, *Whitehouse* 18116 (SMU, US). Kenedy Co.: 6 miles s. of Norias, *Shinners* 17818 (SMU). Kleburg Co.: King's Ranch, *Schulz* 61 (US). La Salle Co.: 10.2 miles n.w. of Cotulla, *Shinners* 17297 (MIN, SMU). Live Oak Co.: 41 miles n. of Alice, *Painter & Barkley* 14462 (TEX). Maverick Co.: 0.6 mile s.e. of Quemado, *Ownbey & Ownbey* 1631 (F, MIN, NY, SMU, TEX, UC); Rio Grande valley near Eagle Pass, alt. 700 ft., *Pringle* 8277 (US, holotype of *A. purpurea* Rose ex Fedde; isotypes, F, GH, MEXU, MIN, MO, ND, NY, PH, POM, RM, UC, US, *A. purpurea* Rose, in herbaria). McMullen Co.: 20 miles s.w. of Tilden, *Rogers, Albers & Webster* 6805 (TEX). Nueces Co.: Corpus Christi, alt. sea level to 40 ft., *Heller* 1378 (F, GH, MIN, MO, NY, RM, UC, US, duplicates of syntype of *A. pinnatifida* Norton); Corpus Christi, *Nealley* 9 (F, holotype of *A. platyceras* var. *rosea* Coulter, i.e., of *A. sanguinea* Greene). Pecos Co.: Mesquite valleys, *Tharp* 43-586, in part (CAS, TEX, UC). Reeves Co.: 1 mile e. of Saragosa, *Cory* 52146 (SMU, US). Refugio Co.: about 6 miles n. of Bayside, *Whitehouse* 21232 (SMU). San Patricio Co.: 6.5 miles s.e. of Sinton, *Ownbey & Ownbey* 1608 (K, KSC, MICH, MIN, SMU, TEX, UC, US). Starr Co.: 8 miles e. of Rio Grande City, *Clover* 192 (MEXU, TEX). Val Verde Co.: 14.9 miles w. of Langtry, *Ownbey & Ownbey* 1637 (MIN, TEX, US). Victoria Co.: 9.7 miles n.e. of Victoria, *Ownbey & Ownbey* 1590 (GA, GH, ILL, MIN, OKL, SMU). Webb Co.: 9 miles s.e. of Laredo, *Ownbey & Ownbey* 1629 (KSC, MIN, OKL, SMU, US). Wilson Co.: 12 miles w. of Floresville, *Cory* 55375 (SMU, US). Zapata Co.: 3.1 miles n.w. of Zapata, *Ownbey & Ownbey* 1628 (MIN, POM, RM, SMU, TEX, US).

MEXICO.

COAHUILA

S. Paila, alt. 1375 m., *Hinton, et al.* 16600 (GH, US); Parras, *Palmer* 20 (GH, NY, US); Parras, *Palmer* 442 (F, GH, MO, NY, UC, US); Saltillo, *Palmer* 564 (F, GH, MO, NY, UC, US); Matamoros, *Pringle* 9191 (US); 12 miles n. of Hipólito, road to Monclova, *White* 1695 (GH).

DURANGO

57.3 miles w. of Gómez Palacio on road through Mapimí, *Ownbey & Ownbey* 1451 (MIN); 17.3 miles s.w. of Ciudad Lerdo on road to Durango, *Ownbey & Ownbey* 1862 (BM, CAS, F, GH, MEXU, MICH, MIN, MO, NY, SMU, UC, US); 4.3 miles s.w. of Cuencamé on road to Durango, *Ownbey & Ownbey* 1864 (GH, MEXU, MIN, US).

NUEVO LEÓN

14.8 miles n. of Vallecillo, *Ownbey & Ownbey* 1402 (MIN); Monterrey, *Trelease* 10 (MO).

18. ARGEMONE **chisosensis** G. B. Ownb., sp. nov.

A. platyceras McDoug. & Sperry, Pl. Big Bend, p. 80. 1951; not *A. platyceras* L. & O.

Herba biennis aut perennis vetustiori aetate caudice robusto et carnoso. Caules 4-8 dm. alti, sparse vel dense aculeati. Alabastra plerumque conspicue aculeata, aculeis robustis perpendicularibus, petalis albis vel pallide purpureis. Capsulae anguste elliptico-lanceolatae vel aliquando elliptico-ovatae, 8-13 mm. latae, 30-45 mm. longae. Semina circa 1.8-2.2 mm. longa.

Biennial or perennial with yellow latex, the older plants with a stout, fleshy caudex; stems 1-few, 4-8 dm. tall, sparingly branched, sparsely to copiously prickly with long, slender, perpendicular prickles; lower leaves lobed to near the midrib, the middle and upper ones usually less deeply lobed, the lobes distant, the larger ones oblong, the margins of the lobes with acute teeth, the lower leaf surfaces stoutly armed on the midvein and less so on the secondaries, the upper surfaces almost smooth or weakly armed on the main veins; buds broadly elliptical, the body 11-15 mm. wide, 15-20 mm. long, mostly moderately prickly with strong, perpendicular prickles, the sepal horns terete, or angular in cross-section, 8-10 (7-12) mm. long, the basal portion usually prickly with perpendicular prickles, the long, indurated apical spine sometimes flattened at its juncture with the herbaceous basal portion; flowers 7-10 cm. in diameter, usually closely subtended by 1-2 foliar bracts; petals white to pale lavender, suborbicular to obcuneate-obovate; stamens about 150 or more, the filaments pale lemon yellow or red, the anthers yellow or purplish; stigma purple, about 2.5-3.5 mm. wide, 1.5-2.5 mm. high; capsules 3-4-carpellate, mostly narrowly elliptic-lanceolate, sometimes elliptic-ovate, the width, excluding the armature, 8-13 mm., the length, including the stigma, 30-45 mm., armed with scattered, stout, spreading or slightly recurved spines interspersed with a few smaller spines and prickles, the largest spines to about 10 mm. long, the capsular surface clearly visible through the armature; seeds about 1.8-2.2 mm. long. (Ill.: Fig. 17, 5-6; Dist.: Fig. 18.)

Holotype: *Roxana S. Ferris & Carl D. Duncan* 3003, collected in Juniper Canyon, Chisos Mountains, Brewster Co., Texas, July 15-18, 1921 (NY; isotypes, CAS, DS, MO).

Habitat and distribution: Arid plains and mountains, often along drainages; evidently in a wide range of soil types; western Texas and adjacent Mexico, at elevations of about 3000-6500 ft.

Flowering and fruiting dates: First flowers usually open by March 15; flowering continues as local conditions permit until December. First fruits mature by April 15 and fruits continue to mature until December.

This taxon, in typical aspect, is set apart by its evidently perennial caudex, bristly stems and buds, long sepal horns and usually narrowly elliptic-lanceolate capsules. Plants collected at higher elevations in the Chisos Mountains area are very distinctive. Collections from peripheral areas, however, exhibit less marked prickliness and other anomalies. In some instances such plants are not easily separated from species occupying adjacent regions, especially *A. sanguinea*. *Palmer* 349, from Aldama, Chihuahua, is even more coarsely armed than the type material. It may be that some of these anomalous elements will ultimately be assigned to other taxa. For this reason I am according *A. chisosensis* specific rank with some hesitancy. More extensive field studies as well as experimental work are a necessary prerequisite to a fuller understanding of this taxon.

Specimens examined: UNITED STATES.

Texas

Brewster Co.: Oak Canyon, Chisos Mts., *Cory* 6994 (GH); Juniper Canyon, Chisos Mts., *Ferris & Duncan* 3003 (NY, holotype of *A. chisosensis* Ownb.; isotypes, CAS, DS, MO); 25 miles n. of Boquillas, *Hanson* 588 (NY, US); Chisos Mts., *Marsh* 107 (F); 25.6 miles s. of Marathon, *Ownbey & Ownbey* 1639 (MIN); Mt. Emory, *Sehultz* 4241 (F); The Basin, Chisos Mts., *Sperry* 383 (US); e. of Nugent Mt., *Sperry* 1369 (US); Glenn Springs, Chisos Mts. area, *Warnock* 146 (TEX); s. of Alpine on Terlingua road, *Whitehouse* 703 (NY, SMU). Culberson Co.: 4.6 miles n.e. of Pine Springs, *Ownbey & Ownbey* 1740 (ARIZ, COLO, GH, MIN, NEW MEX, NY, SMU, TEX, UC, US); s. of Wylie Mts., about 13 miles s.e. of Van Horn, *Waterfall* 5113 (MO); n.e. side of Beach Mt., 7 miles n. of Van Horn, *Waterfall* 4659 (CAS, GH, MO, NY). Hudspeth Co.: Sierra Blanca, *Mulford* 282 (MO); 9 miles n.w. of Sierra Blanca, *Ownbey & Ownbey* 2053 (CAS, F, GH, MIN, MO, POM, RM, SMU); Carrizo Mts., 7 miles w. of Van Horn, *Waterfall* 5052 (GH); Indian Hot Springs, s. of Sierra Blanca, *Whitehouse* 8281 (F). Jeff Davis Co.: Madera Springs, *Whitehouse* 11816 (SMU). Pecos Co.: Ft. Stockton, *Whitehouse* 8280 (F, TEX); mesquite flats, *Tharp* 43-585 (RM, TEX); same loc., *Tharp* 43-586, *in part* (DS, GH). Presidio Co.: 4¾ miles n.e. of Porvenir, *Cory* 53574 (SMU); Alamito Creek on Rio Grande, *Hinckley* 1478 (NY); Van Creek about 2 miles s. of county line, alt. 1050 m., *Hinckley* 1622 (SMU, TEX); near Shafter, *Ingram* 2606 (US); n.e. side of Chinati Mts., *Muller* 8323 (SMU). Reeves Co.: 9¾ miles s. of Balmorhea, *Cory* 18404 (GH); 15.5 miles s.w. of Pecos, *Cory* 52128 (SMU); near Balmorhea, *Whitehouse* 11818 (SMU). Terrell Co.: Sanderson, *Orcutt* 670 (US); 20 miles e. of Dryden, *Parks, Turner & Warnock* 147 (TEX). Val Verde Co.: 5 miles w. of Langtry, alt. 1370 ft., *Warnock & Cameron* 9927 (SMU).

MEXICO.

Chihuahua

Vicinity of Aldama, *Palmer* 249 (NY, US).

Coahuila

Múzquiz, *Marsh* 1052 (F); El Berrendo, near Múzquiz, alt. 4000 ft., *White* 1845 (GH).

19. ARGEMONE CORYMBOSA Greene, in Bull. Calif. Acad. 2: 59. 1886.

Perennial with orange latex; stems cymosely branched, the ultimate branches short, sparsely to moderately armed with stout, perpendicular or recurved spines, densely foliate; leaves coriaceous, green or glaucous, shallowly to deeply lobed, the surfaces smooth to sparingly prickly especially on the midrib beneath; buds subspherical to elliptic-obovate, the body 6-14 mm. broad, 10-18 mm. long, the sepal horns 5-7 mm. long; flowers 4-9 cm. in diameter; petals white; stamens about 100-120, the filaments pale yellow, the anthers yellow; stigma yellowish-green to purple, 3-4 mm. broad, 2.5-3.0 mm. high; capsules ovate to lanceolate, 3-5-carpellate, the width, exclusive of armature, 10-16 mm., the length, including the stigma, 25-35 mm., the surface stoutly and rather evenly, but not closely armed with spreading spines, the largest of which is about 5-7 mm. long; seeds about 1.5-2.0 mm. long.

Holotype: *Mrs. M. K. Curran s.n.* (i.e., Mrs. Katherine Brandegee), Mojave Desert, California, June, 1884 (GH; isotype, UC).[1]

Key to the subspecies:

1. All the leaves shallowly lobed to essentially unlobed; Mojave Desert of California . . . . . 19a. *A. corymbosa subsp. corymbosa*
1. Lower leaves deeply lobed, the middle and upper ones more shallowly lobed; s.e. Utah and n.e. Arizona . . . . . 19b. *A. corymbosa* subsp. *arenicola*

19a. ARGEMONE CORYMBOSA Greene subsp. CORYMBOSA

A. corymbosa Greene, in Bull. Calif. Acad. 2: 59. 1886; Gray, Syn. Fl. N. Am. 1 (1): 88. 1895; Wolf, in Rancho Santa Ana Bot. Gard. Occ. Papers, ser. 1 (2): 59. 1938; Abrams, Ill. Fl. 2: 230. 1944.

A. intermedia var. *typica* Prain, in Journ. Bot. 33: 363. 1895, in small part; not *A. intermedia* Sweet.

A. intermedia var. *corymbosa* Eastwood, in Erythea 4: 96. 1896; Fedde, in Pflanzenr. 4 (104): 282. 1909; Parish, in Bot. Gaz. 65: 337. 1918; Jeps., Fl. Calif. 1: 560. 1922, fig. 116 excluded; Jeps., Man. Fl. Pl. Calif., p. 400. 1925; Munz, Man. S. Calif. Bot., p. 182. 1935; not *A. intermedia* Sweet.

Stems 1-4, 5-8 dm. tall, much branched in the upper parts; leaves green or faintly glaucous beneath, glaucous above, the basal and lower cauline 8-12 (-20) cm. long, obovate to oblanceolate, shallowly lobed, the apices of the lobes rounded, the middle and upper cauline leaves progressively smaller and successively obovate, elliptical and ovate, more shallowly to very shallowly if at all lobed, the margins of all the leaves sparingly prickly with stout prickles, the broad bases of the upper cauline leaves clasping the stem, the leaf surfaces sparingly but stoutly prickly on the main veins beneath, smooth or very sparingly and more weakly prickly on the midrib and main veins above; buds subspherical to elliptic-obovate, the body 10-14 mm. broad, 12-16 mm. long, sparingly prickly with spreading prickles; flowers 5-9 cm. in diameter; stigmas evidently purple, about 3.0 mm. broad and 2.5 mm. high; capsules 4-5-carpellate, ovate to lanceolate, the width, excluding the armature, 10-15 mm., the length, including the stigma, 25-30 mm., stoutly and rather evenly but not closely spinescent, the largest spines usually 6-7 mm. long; seeds bluish-black, usually just over 1.5 mm. long. (Ill.: Fig. 19, 1-3; Dist.: Fig. 25.)

Holotype: That of the species.

Habitat and distribution: Dry, open flats, slopes, stabilized dunes and

[1] Wolf (1938) expresses the opinion that Kelso is the type locality of this species. This may be true since Mrs. Brandegee is known to have collected it there in 1917. However, she had also collected the species at Nipton in 1915, and this or elsewhere on the Mojave might actually be the type locality.

washes, sandy or granitic soils, Mohave Desert, San Bernardino Co., Calif., at altitudes of about 1400-3000 ft.

Flowering and fruiting dates: Flowering begins in late March or early April; fruits mature from about May 15 through June.

A. corymbosa subsp. *corymbosa* is distinguished by its sparingly, coarsely prickly, stout, cymosely much branched stems, the short and numerous ultimate branches of which lend a congested appearance to the inflorescence, and by the dense foliage, the leaves being coriaceous, shallowly lobed or subentire and the broad bases of the upper ones often clasping. The ovate-lanceolate, rather evenly and stoutly spinescent capsules are also very characteristic.

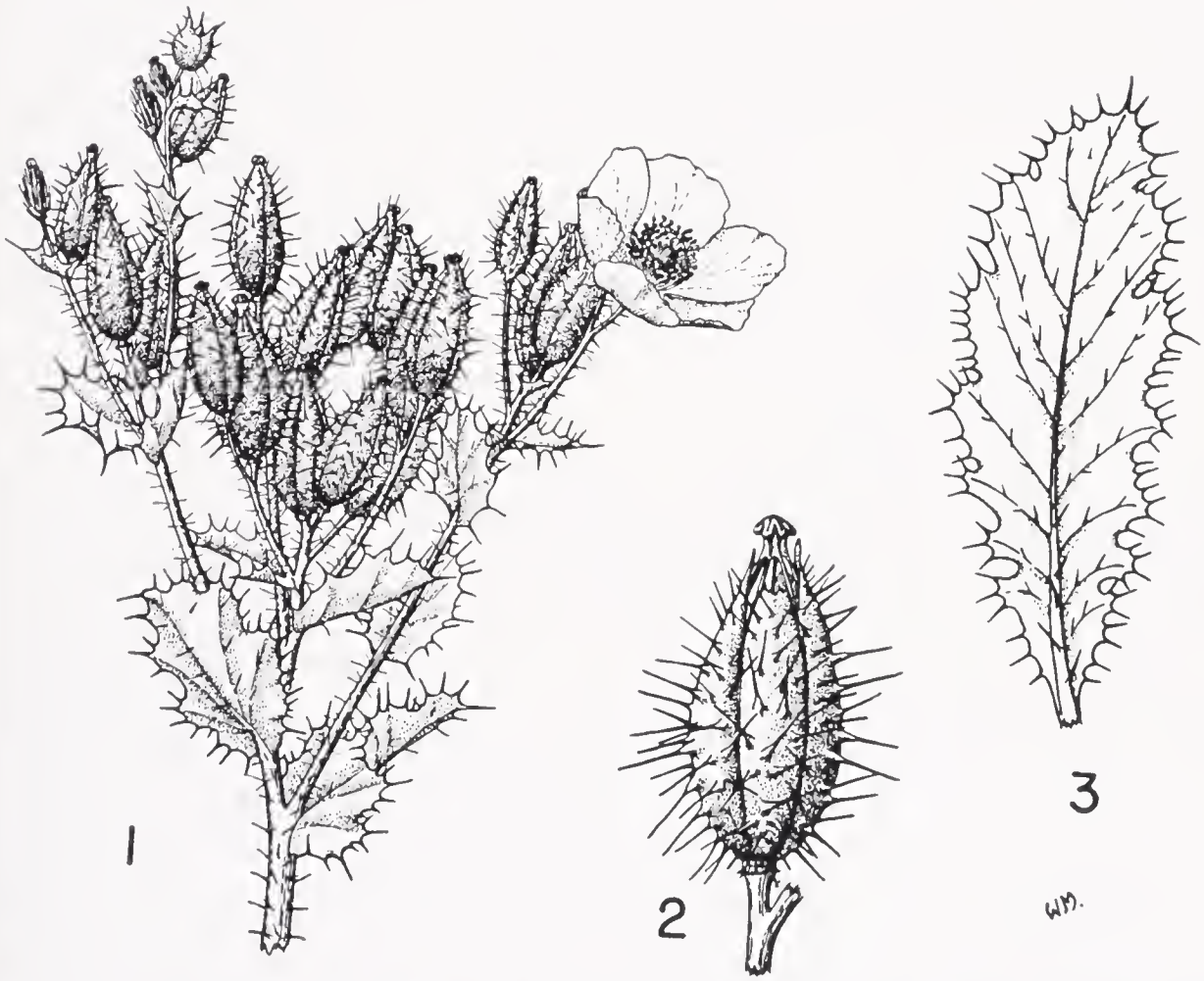

FIG. 19. *A. corymbosa* subsp. *corymbosa*. 1. Habit × ½. *Ownbey & Ownbey* 2130 (MIN). 2. Capsule × 1. *Wolf & Johnson* 8766 (US). 3. Cauline leaf × ½. Same as 1.

This, the originally described component of the species, has been little known except by western botanists. Prain through lack of knowledge and specimens included the species in synonymy under his collective taxon *A. intermedia* var. *typica*. It has been accorded full species rank by Ameri-

can taxonomists with the exception of Miss Eastwood who unjustifiably reduced it to varietal status under *A. intermedia* (auct., non Sweet, i.e., *A. polyanthemos*). Fedde followed Eastwood in making it a variety of *A. intermedia*. Wolf, who was well acquainted with the taxon in the field, correctly allowed it the status of full species.

Specimens examined: UNITED STATES.

CALIFORNIA

Kern Co.: ca. 8 miles n. of Johannesburg, *Gifford s.n.* (DAV). San Bernardino Co.: Granitic slopes on s. side of Cronise Valley, U. S. Hwy. 91, *Abrams* 14011 (DS, GH); Nipton, *Brandegee s.n.* (UC); Kelso, *Brandegee s.n.* (CAS, DS, GH, POM, UC, US); along Mojave River, *Cooper s.n.* (US); Mohave Desert, *Curran s.n.* (GH, holotype of *A. corymbosa* Greene; isotype, capsules only, UC); Black's ranch, s.e. of Fremont's Peak, *Hall & Chandler* 6848 (UC); Mojave Desert, *Morse s.n.* (NY); eastern Mojave Desert, 3 miles w. of Nipton, alt. 3000 ft., *Munz* 11699 (DS, RSA); 2.4 miles s. of Kelso, alt. about 2200 ft., *Ownbey & Ownbey* 2130 (ARIZ, CAS, COLO, F, GH, K, MIN, MO, NY, RM, UC, US); Silver Lake, *Parish* 10372 (DS); 6 miles e. of Lucerne Valley, Mojave Desert, alt. 3000 ft., *Roos & Roos* 4304 (RSA); Mojave Desert, 1 mile e. of Pisgah, *Wolf* 8544 (CAS, DS, POM, RSA, UC); same locality, *Wolf & Johnson* 8766 (CAS, DS, RSA, UC, US); 7 miles s. of Kelso on Amboy road, alt. about 2500 ft., *Wolf* 10190 (RSA, UC); 10 miles s.e. of Baker on road to Kelso, alt. about 1400 ft., *Wolf* 10274 (RSA, UC); Cronise Valley on U. S. Hwy. 91 between Baker and Yermo, alt. ca. 1000 ft., *Wolf* 10328 (DS, RSA); 8 miles n. of Valley Wells on road to Kingston, alt. ca. 3300 ft., *Wolf* 1033 (RSA).

19b. ARGEMONE CORYMBOSA Greene subsp. **arenicola** G. B. Ownb., subsp. nov.

Herba perennis latice aurantiaco. Caules 1-5 (-15), 2-6 dm. alti. Folia crassa coriaceaque, lobata, sinibus usque ½-⅘ spatium ad costam extendentibus, superficie subter ad costam aculeis paucis, supra inermia aut 1-4 aculeis tenuibus. Stigma flavo-viride aut purpurans. Capsulae lanceo-ovatae, 3-5-carpellatae. Semina circa 2.0 mm. longa.

Stems 1-5 (-15), 2-6 dm. tall, moderately branched, green, rarely tinged with pink; leaves glaucous or green below, green or slightly glaucous above, the basal ones 8-15 cm. long, oblanceolate, lobed, the sinuses extending from one-half to four-fifths the distance to the midrib, the lobes oblong, the middle and upper cauline ones elliptical to lance-ovate, more shallowly lobed, the uppermost tending to half-clasp the stem, the margins of all the leaves with deltoid teeth, the leaf surfaces with a few stout prickles on the main veins beneath, smooth or with 1-4 fine prickles above; buds obovate to elliptical, the body 6-12 mm. broad, 10-18 mm. long, sometimes tinged with pink, the surface moderately armed with distant, divergent, perpendicular prickles, the sepal horns sometimes flattened in a tangential plane; flowers 4-8 cm. in diameter; outer petals as broad as long, suborbicular, erose on the distal margin, the inner ones broadly suborbicular-obcuneate, much broader than long, similarly erose distally; stamens surpassed by the ovary; stigmas yellowish-green or purplish, sinuate, about 4 mm. broad and 3 mm. high; capsules 3-4 (-5) -carpellate, lance-ovate, the width, excluding the armature, 14-16 mm., the length, including the stigma, 25-35 mm., stoutly armed with even-sized, large, spreading spines, the largest of which are usually 5-6 mm. long; seeds bluish-black, about 2.0 mm. long. (Ill.: Fig. 20, 1-5; Dist.: Fig. 25.)

Holotype: *G. B. Ownbey and Findley Ownbey* 2146, collected 37.9 miles southwest of Green River, on the road to Hanksville, in rust-colored sand

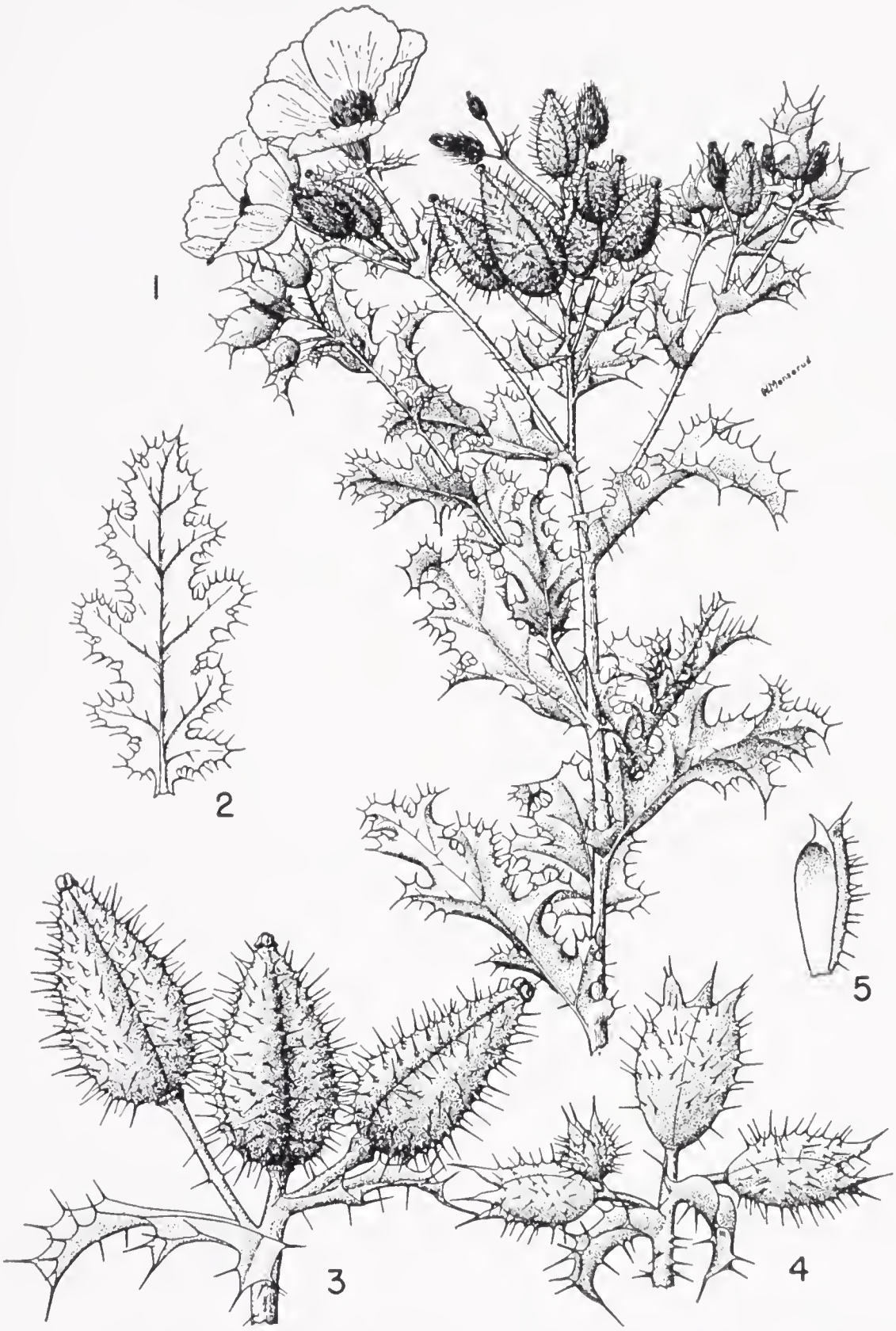

FIG. 20. *A. corymbosa* subsp. *arenicola*. 1. Habit × ½. Holotype, *Ownbey & Ownbey* 2146 (MIN). 2. Cauline leaf × ½. Same as 1. 3. Capsules × 1. Liquid preserved material from type collection; same as 1 (MIN). 4. Buds × 1. Same as 3. 5. Sepal × 1. Same as 3.

dune areas, Emery Co., Utah, June 7, 1954 (MIN; isotypes, ARIZ, BRY, CAS, COLO, DAO, F, GH, K, MEXU, MICH, MIN, MO, NEW MEX, NY, OKL, POM, RM, RSA, SMU, TEX, UC, UTC, US, WS).

Habitat and distribution: Dry desert valleys and plains, especially in areas of stabilized sand or actively moving sand dunes, southeastern Utah and northeastern Arizona, at altitudes of 3000-5000 ft.

Flowering and fruiting dates: Flowering begins about May 1; fruits begin to mature about June 1; under favorable conditions a second flowering and fruiting period may occur during the summer and autumn months.

In the past, specimens of this subspecies have been variously identified as *A. intermedia, A. hispida, A. platyceras* and *A. corymbosa*. It differs from subsp. *corymbosa* in general aspect due to its smaller stature and greater average number of stems from the base, in its tendency to be less profusely branched at the top, and especially in its more deeply cut leaves. It is certainly deserving of at least subspecies rank.

A. corymbosa subsp. *arenicola* almost always occurs in actively moving or stabilized rust-colored sand. It is abundant at the type locality.

Specimens examined: UNITED STATES.

ARIZONA

Coconino Co.: Houserock Valley, *Eastwood & Howell* 6984 (CAS); in desert just w. of Lees Ferry, *McKelvey* 4448 (GH); Navajo Bridge to House Rock Valley, alt. 5100 ft., *Kearney & Peebles* 13622 (NY, US); 11.2 miles s. of "The Gap" (Hwy. 89), *Ownbey & Ownbey* 1813 (ARIZ, COLO, GH, MIN, NEW MEX, POM, RM, UC, UTC, US); 13.2 miles s. of Navajo Bridge, *Ownbey & Ownbey* 1814 (BRY, CAS, MIN, NY, RSA, WIS); 11.6 miles s.w. of Navajo Bridge, *Ownbey & Ownbey* 1815 (ARIZ, GH, MICH, MIN, OKL, SMU, WS); 21.8 miles s.w. of Navajo Bridge (Hwy. 89), *Ownbey & Ownbey* 1815a (COLO, K, MIN, TEX); 9.9 miles s.w. of Tuba City on road to Hwy. 89, *Ownbey & Ownbey* 2165 (ARIZ, CAS, COLO, GH, MIN, MO, RSA, SMU, UC, UTC, US, WS); near Navajo Bridge, alt. 3400 ft., *Peebles* 13019 (US); same locality, alt. 3900 ft., *Peebles* 13022 (US).

UTAH

Emery Co.: 37.9 miles s.w. of Green River on road to Hanksville, *Ownbey & Ownbey* 2146 (MIN, holotype of *A. corymbosa* subsp. *arenicola* Ownb.; isotypes, ARIZ, BRY, CAS, COLO, DAO, F, GH, K, MEXU, MICH, MIN, MO, NEW MEX, NY, OKL, POM, RM, RSA, SMU, TEX, UC, UTC, US, WS). Grand Co.: Grand River near Moab, *Jones s.n.* (CAS, GH, NY, US); 4.9 miles n.w. of Moab, Hwy. 160, *Ownbey & Ownbey* 2160 (ARIZ, GH, MIN, UTC); s. of Cisco, alt. 4100 ft., *Ripley & Barneby* 5414 (CAS). Iron Co.: Cedar Canyon, *Garrett* 6073 (RM), a doubtful record. Kane Co.: Kaiparowits Plateau, *Tompkins s.n.* (CAS). San Juan Co.: 4 miles s.w. of Bluff, *Ownbey & Ownbey* 2161 (MIN); 21.8 miles s.w. of Bluff, Hwy. 47, *Ownbey & Ownbey* 2164 (ARIZ, COLO, GH, K, MIN, MO, NY, POM, RM, UC, UTC, US).

20. ARGEMONE GRACILENTA Greene, in Pittonia 3: 346. 1898.

A. gracilenta Rose, in Contr. U. S. Nat. Herb. 8: 27. 1903.

A. albiflora Wats., in Proc. Am. Acad. 24: 38. 1888; not *A. albiflora* Hornem.

A. intermedia var. *typica* Prain, in Journ. Bot. 33: 363. 1895, in part; not *A. intermedia* Sweet.

A. intermedia var. *typica* Prain "ssp. *parviflora*" Prain, l.c., p. 364, nomen nudum; not *A. intermedia* Sweet.

A. platyceras var. *gracilenta* Fedde, in Pflanzenr. 4 (104): 285. 1909; Johnston, in Proc. Calif. Acad. 12: 1024. 1924; not *A. platyceras* L. & O.

A. intermedia Kearn. & Peeb., Fl. Pl. Ariz., p. 336. 1942, in part; Kearn. & Peeb., Ariz. Fl., p. 324. 1951, in part, as to Arizona; not *A. intermedia* Sweet.

Perennial with very pale yellow, almost white or rarely distinctly yellow latex; stems usually 1-6, 4-12 (-18) dm. tall, openly branched, moderately but conspicuously prickly throughout with usually very long, perpendicular prickles; leaves very glaucous, sublinear to elliptic-oblong, the basal ones to about 4 dm. long, often deeply lobed, the cauline sometimes deeply, but more often shallowly lobed, each marginal tooth terminated by a long, slender prickle, the lower surfaces of the leaves moderately prickly on the main veins, the upper surfaces very sparsely prickly on the midrib to entirely smooth; buds subspherical to oblong, the body 12-15 mm. broad, 15-18 mm. long, smaller during the dry season, sparingly prickly with perpendicular prickles, the sepal horns terete, usually long and slender, the length 8-12 (5-14) mm., usually wholly smooth but sometimes with 1 or 2 prickles near the base, the terminal spine elongate; flowers 6-9 cm. in diameter or smaller; petals white; stamens about 150, the filaments pale yellow, the anthers yellow; stigma purple, to about 4 mm. broad and 3 mm. high, often considerably smaller; capsules 3-4-carpellate, narrowly elliptical to narrowly elliptic-ovate, the body, exclusive of spines, 8-14 mm. broad, the length, including the stigma, 30-45 (-50) mm., sparingly armed with spreading spines, the longest of which is usually 6-8 (-10) mm.; seeds to 2 mm. long, often appreciably less. (Ill.: Fig. 21, 1-5; Dist.: Fig. 25.)

Lectotype: *Edward Palmer* 7, collected at Mulegé, Gulf of California, Baja California, Mexico, June, 1887 (ND; isotypes, DS, GH, NY US).

Habitat and distribution: Sandy and gravelly washes, outwash plains, dry, flat, eroded, desert terrain, west-central Arizona southward in the Sonoran Desert to Baja California del Sur, at elevations of near sea level to about 3000 ft., but mainly below 1000 ft.

Flowering and fruiting dates: In the north flowering begins about March 15 and first fruits mature about the end of April; in the south flowering begins about Feb. 1, and first fruits are matured early in March. Flowering and fruiting continues as conditions permit through November.

This species is distinguished by the nearly white latex, the ordinarily shallowly lobed or undulate-margined cauline leaves, the subspherical buds, the long, terete sepal horns which are usually totally smooth, and by the rather sparse, long and slender prickles of the stem.

When describing this species Greene made no mention of the similarity of the Mulegé specimens to the common prickly poppy of the Sonoran Desert. I can find no fundamental difference between the plants from Lower California and those from Sonora and Arizona and am, therefore, broadening the species circumscription to include these latter components.

There is considerable doubt of the genetic "purity" of *A. gracilenta* from certain localities in northern Sonora and Arizona. In southern Arizona and northern Sonora it appears to hybridize with *A. pleiacantha* subsp. *pleiacantha,* particularly in the vicinity of Tucson, Arizona. It

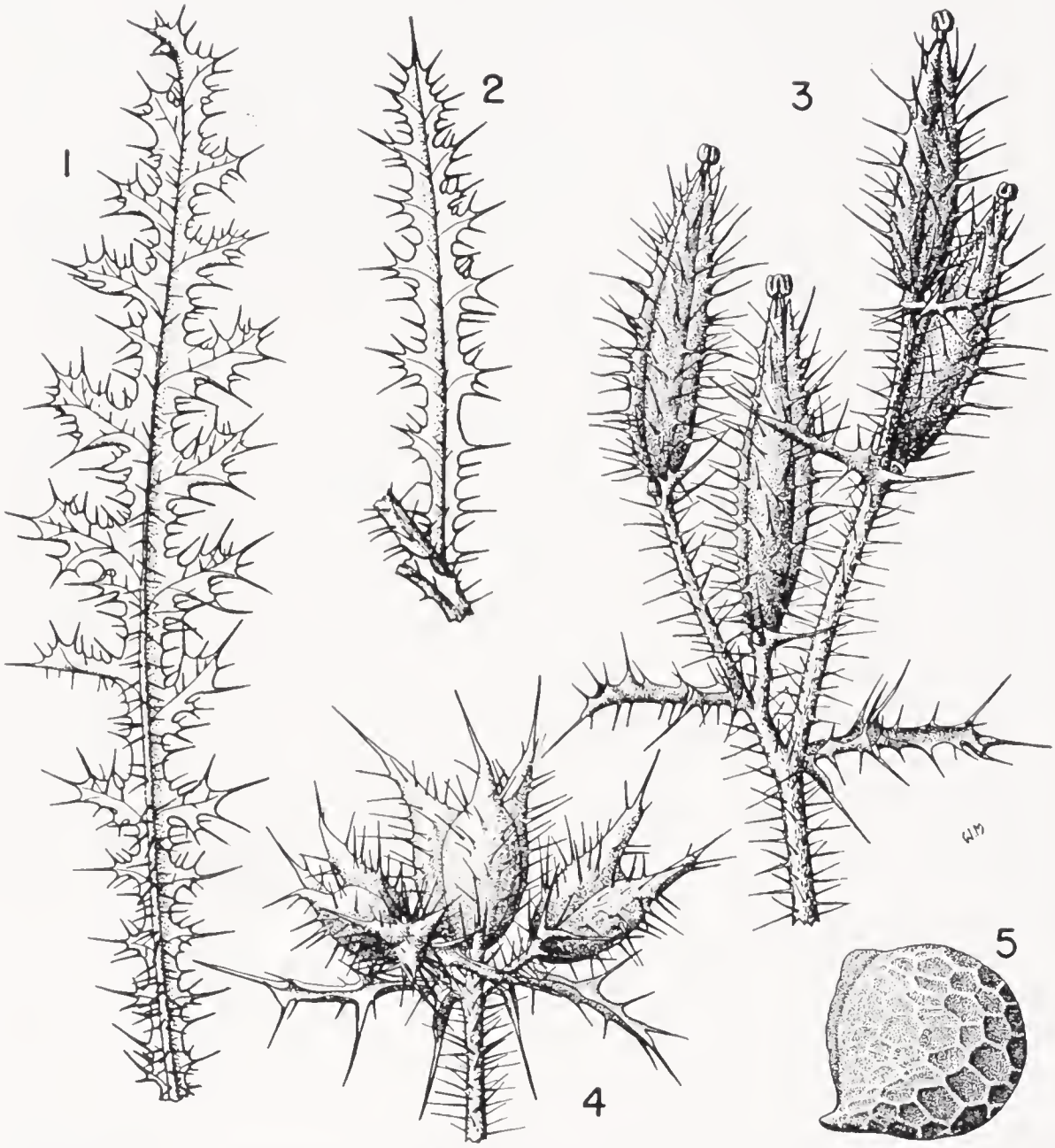

FIG. 21. *A. gracilenta*. 1. Basal leaf, under surface × ½. *Ownbey & Ownbey* 2087 (MIN). 2. Cauline leaf, upper surface × ½. *Ownbey & Ownbey* 2084 (MIN). 3. Capsules × 1. *Ownbey & Ownbey* 2079 (MIN). 4. Buds × 1. Same as 3. 5. Seed × 15. Topotype, *Johnston* 3665 (GH).

appears to hybridize with *A. pleiacantha* subsp. *ambigua* along the western periphery of the plateau region of central Arizona where the plateau drops off abruptly into the desert, that is, in Yavapai, northern Maricopa, and east-central Mojave counties. The fact that all three of these taxa are diploids lends credibility to an hypothesis of possible natural hybridization among them. For a further discussion see the text under *A. pleiacantha*. Over most of their ranges *A. gracilenta* and *A. pleiacantha* are well separated geographically and ecologically, and the two species are perfectly distinct.

The relationships of *A. gracilenta* to other species of *Argemone* are incompletely understood. In addition to a probable relationship to *A. pleiacantha* as indicated above, it is probably also rather closely related to *A. munita*, especially subspp. *munita* and *robusta*, and to other white-flowered species, e.g., *A. polyanthemos*.

In Prain's monograph the type collection of *A. gracilenta* is cited under *A. intermedia* var. *typica*. Following Greene's lead, however, Fedde recognized *A. gracilenta*, but reduced it to varietal status under *A. platyceras*, a view which cannot be supported on any grounds.

Specimens examined: UNITED STATES.

Arizona

Maricopa Co.: Agua Caliente, *Carlson s.n.* (CAS); 20.6 miles s. of Rock Springs, *Ownbey & Ownbey* 2099 (COLO, GH, MICH, MIN); 1.8 miles n.e. of Aguila, *Ownbey & Ownbey* 2109 (BRY, MEXU, MICH, MIN, NY, RM, SMU, UC, UTC); 5 miles e. of Gila Bend, alt. 680 ft., *Wolf* 2304 (CAS, DS, GH, RSA). Mohave Co.: Aquarius Mts., *Eastwood* 18377 (CAS). Pima Co.: desert w. of Tucson Mts., alt. about 2500 ft., *Graham s.n.* (NY, UC); fenced area, Santa Rita Forest Reserve, *Griffiths* 3858 (UC); near Tucson, *Peebles* 1564 (US); Tucson, *Rose* 11832 (NY, US); roadsides, Tucson, alt. 2400 ft., *Shreve* 10195 (DS, UC); mesas, Wilmot, alt. 2600 ft., *Thornber* 484 (MIN, MO, UC, US). Pinal Co.: roadside, Santan Mts., *Harrison & Kearney* 8683 (F); 7.3 miles s.e. of Picacho, *Ownbey & Ownbey* 1793 (ARIZ, CAS, COLO, GH, K, MIN, NY, RM, UC, US, UTC); 12.8 miles n. of Florence, *Ownbey & Ownbey* 1832 (MIN); Casa Grande, *Peebles & Harrison* 1867 (US). Yavapai Co.: 3.9 miles n.e. of Congress, *Ownbey & Ownbey* 2106 (ARIZ, CAS, MIN, NEW MEX, RM). Yuma Co.: 2.8 miles s.w. of Wenden, *Ownbey & Ownbey* 2110 (MIN).

MEXICO.

Baja California

Comondú, *Brandegee s.n.* (UC); 2 miles n. of Mulegé on the Santa Rosalía road, *Ferris* 8684 (DS, NY, POM, US); Mulegé, *Johnston* 3665 (CAS, GH, UC, US); middle w. side, Catalina Island, *Johnston* 4104 (CAS); Santa Catalina Island, *Moran* 3872 (DS); Mulegé, *Palmer* 7 (ND, lectotype of *A. gracilenta* Greene; isotypes, DS, GH, NY, US); Mulegé, *Rose* 16665 (NY, US); 11 miles e. of San Ignacio, *Wiggins* 7910 (DS, US).

Sonora

La Colorado, *Clokey* 1932 (UC); beside Guaymas road, about 3 km. s. of Villa de Seris, *Drouet & Richards* 3772 (DS, F); 43 km. (27 miles) n. of Hermosillo on road to Nogales, *Frye & Frye* 2293 (DS, GH, MO, NY, RM, RSA, UC, US); Ciudad Obregón, *Gentry* 277 (DS); near Pieú Pass, *Long* 40 (US); Charco, s. of Sierra Blanca, *Lumholtz* 22 (GH); 2 miles s. of Hermosillo, *Ownbey & Ownbey* 1758 (GH, MEXU, MIN, NY, UC, US); 13.6 miles n. of Guaymas, *Ownbey & Ownbey* 1759 (ARIZ, CAS, GH, MEXU, MICH, MIN, MO, UC, US); 70.7 miles s. of Magdalena on road to Hermosillo, *Ownbey & Ownbey* 1761 (COLO, DAO, F, K, MEXU, MIN, NEW MEX, POM, WS); 13.2 miles s. of Santa Ana on road to Hermosillo, *Ownbey & Ownbey* 1762 (GH, MEXU, MIN); vicinity of Hermosillo, *Rose, Standley & Russell* 12373 (GH, NY, US); Los Ranchos, vicinity of Guaymas, *Rose, Standley & Russell* 15044 (NY, US); 11 miles e. of Willard between Hermosillo and Colorado, *Wiggins & Rollins* 296 (DS, MO, ND, GH, NY, US); about opposite Carbó on new highway, *Wiggins* 7527 (DS, US); 11 miles n. of San Pedro Rancho (16.9 miles n.w. of Tajitos), *Wiggins* 8300 (DS, UC, US).

21. ARGEMONE GRANDIFLORA Sweet, Brit. Fl. Gard. 3: t. 226. 1829.

Annual or short-lived perennial with yellow latex; stems 1-few, 3-12 (-15 or more) dm. tall, openly and widely branched, totally smooth to prickly throughout with scattered prickles (in subsp. *armata*); basal and lower cauline leaves deeply lobed, the middle and upper cauline progressively less deeply lobed and with fewer lobes, all the lobes with marginal lanceolate, prickle-tipped teeth, the lower surfaces of the leaves smooth or distantly prickly on the veins or (in subsp. *armata*) with a few stoutish prickles on the main veins, the upper surfaces smooth or with a few weak prickles on the main veins; buds subspherical, the body 12-17 mm. broad, 14-20 mm. long, smooth or armed with a few scattered, spreading prickles (especially in subsp. *armata*), the sepal horns terete, 7-15 mm. long, usually totally smooth, spine-tipped; flowers 6-10 cm. across, closely to distantly subtended by 1-2 bracteate leaves; petals white, suborbicular to broadly obovate-obcuneate; stamens at least 150, often many more, the filaments lemon-yellow, the anthers bright yellow; stigma purple, about 2.5-5.0 mm. wide and 1.5-3.0 mm. high; capsules 3-5-carpellate, broadly oblong to elliptical, the width, exclusive of armature, 10-18 mm., the length, including the stigma, 20-40 mm., armed with a few scattered, stoutish, spreading or recurved, even-sized spines and (in subsp. *armata*) sometimes with a few lesser spines and prickles, the largest spines about 5 (-8) mm. long, the capsular surface always clearly visible through the armature; seeds 1.8-2.2 mm. long.

Holotype: Sweet, l.c., states: "For the opportunity afforded us of giving a figure of this grand plant, we are obliged to the kindness of Robert Barelay, Esq. of Bury Hill, in whose superb collection it was raised this Spring, from seeds received from Mexico." Prain (1895, p. 333) notes that the "types" of Sweet's figures are preserved at Kew. There are, indeed, two sheets of *A. grandiflora*, cultivated in Barclay's garden, preserved at Kew. I know of no way positively to prove that these specimens actually represent those from which the original description and illustration were drawn, but the circumstantial evidence in favor of this view is strong. I have, therefore, designated these specimens the holotype. The exact identity of *A. grandiflora* can never be in doubt since the species was well illustrated in the original publication and in other journals of the period.

This species is easily separable into two components, viz., the historically well known *A. grandiflora* herein treated as subsp. *grandiflora*, and the previously undescribed subsp. *armata*. Distributionally, the latter subspecies occurs to the north of the former. Plants of the latter are, on the average, of much lower stature and have smaller leaves. These two subspecies have been studied extensively in the experimental garden by the writer. There appear to be no important sterility barriers between them under experimental conditions.

Key to the subspecies:

1. Stems smooth or with very few scattered prickles; leaves entirely smooth on both surfaces or distantly prickly on the veins beneath and rarely also with a very few prickles above . . . . . 21a. *A. grandiflora* subsp *grandiflora*

1. Stems prickly throughout with scattered prickles; lower surfaces of the leaves with a

few stoutish prickles on the main veins, the upper surfaces smooth or weakly prickly on the main veins . . . . . 21b. *A. grandiflora* subsp. *armata*

21a. ARGEMONE GRANDIFLORA Sweet subsp. GRANDIFLORA

A. grandiflora Sweet, Brit. Fl. Gard. 3: t. 226. 1829; Lindl., in Edwards's Bot. Reg. 15: t. 1264. 1829; Loddig., Bot. Cab. 16: t. 1546. 1829; Loud., in Gard. Mag. 6: 115. 1830; Loud., Hort. Brit., p. 216. 1830; Hook., in Curtis's Bot. Mag. 58: t. 3073. 1831; Otto & Dietr., in Allgem. Gartenzeit. 1: 300. 1833; Spach, Hist. Nat. Vég. 7: 27. 1839; Walp., Rep. 1: 110. 1842; Hemsl., Biol. Cent. Am., Bot. 1: 26. 1879; Prantl & Kündig, in Engl. & Prantl, Nat. Pflanzenf. 3 (2): 141. 1889; Prain, in Journ. Bot. 33: 332. 1895; Gray, Syn. Fl. N. Am. 1 (1): 87. 1895; Rose, in Contr. U. S. Nat. Herb. 8: 25. 1903; Fitzh., in Gard. Chron., third ser., 42: 113. 1907; Fedde, in Pflanzenr. 4 (104): 280, 274, fig. 36H, L. 1909.

A. mexicana Baillon, Hist. Pl. 3: 113, figs. 125-127. 1871, excluding fig. 127 which is undeterminable; not *A. mexicana* L.

Stems commonly 1, 6-12 (-15 or more) dm. tall, totally smooth or with a very few scattered prickles; lower cauline leaves often to 40 cm. or more long and 15 cm. or more wide, deeply lobed, the middle and upper leaves progressively smaller and more shallowly lobed, the marginal teeth of all the leaves large, few, broadly lanceolate, the leaf surfaces smooth or very distantly prickly on the veins beneath, usually totally smooth above; body of the buds about 13-17 mm. broad, 15-20 mm. long, smooth or sometimes with 1-4 weak prickles on each sepal, the sepal horns 7-15 mm. long, smooth; flowers 6-10 cm. across, usually not closely subtended by bracteate leaves; petals suborbicular to broadly obovate; stigma about 3-5 mm. wide and 2-3 mm. high; capsules broadly oblong-elliptic, the width, exclusive of spines, 10-18 mm., the length, including the stigma, 20-40 mm., armed with a few stout, spreading, subequal spines, the largest spines to about 5 mm. long, the capsular surface otherwise essentially smooth; seeds about 1.8-2.2 mm. long. (Ill.: Fig. 22, 1-3; Dist.: Fig. 25.)

Holotype: That of the species.

Habitat and distribution: Hills, mountains and adjacent flat lands, often in disturbed soils of roadways and around habitations at altitudes of near sea level to possibly 6000 ft. or more; east-central Mexico, Hidalgo to southern Tamaulipas. The species appears to be native in Hidalgo at intermediate elevations, and many of the peripheral records are surely introductions.

Flowering and fruiting dates: May be found in flower and fruit throughout the year; at higher elevations, however, the period of greatest abundance appears to be June, July and August.

This subspecies is best characterized by the near or complete lack of prickles on the leaf surfaces and stem, by the subspherical, smooth or nearly smooth buds with long sepal horns, and by the sparingly spinescent capsules. It is perhaps the most distinctive of all of the white-flowered forms of *Argemone*.

Specimens examined: MEXICO.

HIDALGO

Jacala, alt. 4500 ft., *Chase* 7102 (F, GH, MO, NY); vicinity of Zimapán, *Kenoyer* 1035 (GH); 18.5 miles n.e. of Jacala, *Ownbey & Ownbey* 1419 (F, GH, MEXU, MIN, NY, UC, US); 9 miles n. of Zimapán, *Ownbey & Ownbey* 1420 (CAS, K, MICH, MIN,

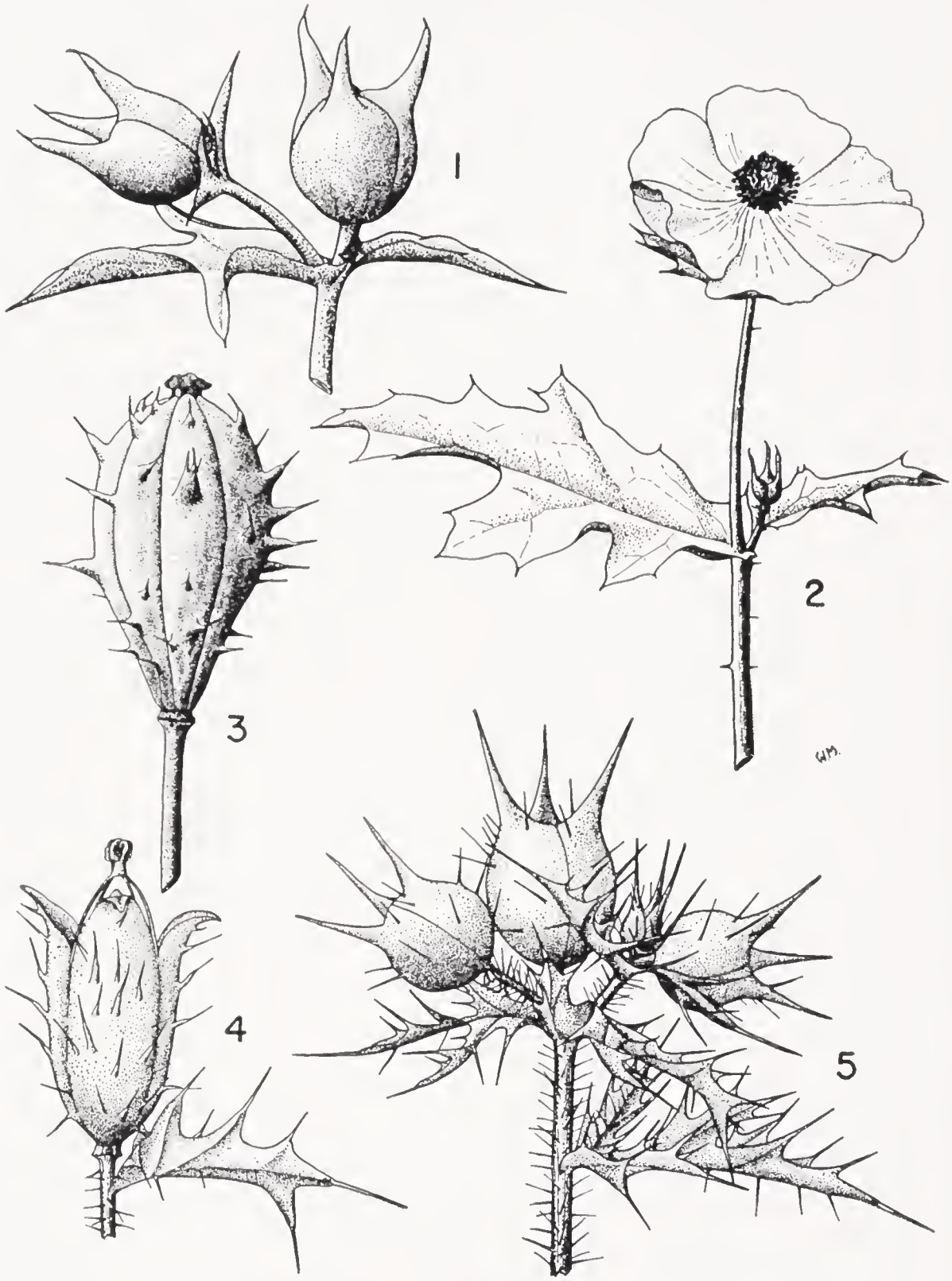

FIG. 22. 1-3. *A. grandiflora* subsp. *grandiflora*. 1. Buds × 1. Cult. from seeds collected at El Pinalito, Hidalgo, *Straw* M18 (MIN). 2. Flower × ½. Same as 1. 3. Fruit × 1. Same as 1. 4-5. *A. grandiflora* subsp. *armata*. 4. Capsule × 1. Holotype, *Palmer 57, in part* (US). 5. Buds × 1. *Ownbey & Ownbey* 1411 (MIN).

MO); 6.6 miles n.e. of Jacala, *Ownbey & Ownbey* 2047 (MIN); Sierra de la Mesa, *Rose, Painter & Rose* 9116 (GH, US).

QUERÉTARO

Between Higuerillas and San Pablo, *Rose, Painter & Rose* 9812 (US).

SAN LUIS POTOSÍ

Near Tanquián, *Loesener* 264 (GH, US); near Tancanhuitz, *Nelson* 4408 (GH, US); 14 miles n.w. of Ciudad del Maíz, *Ownbey & Ownbey* 2043 (COLO, GH, K, MEXU, MIN, NY, POM, RM, UC, US, WS); 13.3 miles w. of Río Verde, *Robinson* 64 (US).

TAMAULIPAS

Gómez Farías, *Harrell* 362 (MIN); El Limón, *Ownbey & Ownbey* 1415 (GH, MEXU, MIN); vicinity of La Barra, 8 km. e. of Tampico, *Palmer* 303 (CAS, F, GH, MO, NY, US).

21b. ARGEMONE GRANDIFLORA Sweet subsp. **armata** G. B. Ownb., subsp. nov.

A. intermedia Fedde, in Pflanzenr. 4 (104): 281. 1909, in part; not *A. intermedia* Sweet.

Herba annua. Caules omnino aculeati aculeis dispersis. Folia subter in venis principalibus aculeata supra in venis inermia aut sparse aculeata. Alabastra subglobosa aculeis paucis et dispersis armata, petalis albis. Capsulae oblongae vel late aut anguste ellipticae, spinis robustis patentibus aut reflexis armatae. Semina circa 2.0-2.2 mm. longa.

Stems 1-few, 3-7 dm. tall, prickly throughout with scattered prickles; leaves commonly lobed one-half to three-fourths the distance to the midrib, the lobes lanceolate, the leaf surfaces with a few stout prickles on the main veins beneath, smooth or with a few weak prickles on the main veins above; body of the buds 12-16 mm. broad, 14-18 mm. long, armed with a few scattered, spreading prickles mainly on the upper half, the sepal horns 7-12 mm. long, usually totally smooth; flowers 7-10 cm. across, usually closely subtended by 1-2 bracteate leaves; petals obovate-obcuneate; stigma about 2.5-4.0 mm. wide, 1.5-2.5 mm. high; capsules typically oblong, sometimes broadly to narrowly elliptical, the width, exclusive of armature, 12-16 mm., the length, including the stigma, 25-40 (20-) mm., armed with scattered, stout, spreading or recurved, even-sized spines and sometimes also with a few lesser spines and prickles, the largest spines 6-8 mm. long; seeds about 2.0-2.2 mm. long. (Ill.: Fig. 22, 4-5; Dist.: Fig. 25.)

Holotype: *Dr. Edward Palmer* 57, *in part*, collected in the vicinity of Victoria, altitude abont 320 meters, Tamaulipas, Mexico, Feb. 1 to April 9, 1907 (US; isotypes, F, GH, K, MO, NY).

Habitat and distribution: Fields and waste places, disturbed soil, Tamaulipas, Nuevo León and southern Coahuila, Mexico; in Coahuila almost certainly by introduction; at elevations of 1000-4000 ft.

Flowering and fruiting dates: Only fragmentary information is available; flowering specimens have been collected from March to October; fruiting specimens have been collected from June onward.

This subspecies is best characterized by the distantly prickly stems and by the presence of prickles on the main veins of the under surfaces of the leaves. It is separated from other white-flowered Mexican species of *Argemone* by means of the subspherical, sparingly prickly buds with

long, terete sepal horns and by the armature of the capsules which consists almost entirely of large spines, there being few if any lesser spines and prickles.

Specimens examined: MEXICO.

COAHUILA

2.1 miles w. of San Pedro, *Ownbey & Ownbey* 1449 (MIN, UC).

NUEVO LEÓN

Río Sta. Catarina, Monterrey, *Abbon & Arsène* 6233 (US); outskirts of Sta. Catarina, *Ownbey & Ownbey* 1406 (GH, MIN, NY, US).

TAMAULIPAS

Hacienda Santa Engracia, 40 miles n.w. of C. Victoria, alt. 240 m., *Meyer & Rogers* 2836, *in part* (MIN, MO); 22.3 miles n.w. of C. Victoria, *Ownbey & Ownbey* 1411 (MIN); vicinity of Victoria, alt. 320 m., *Palmer* 57, in part (US, holotype of *A. grandiflora* subsp. *armata* Ownb.; isotypes, F, GH, K, MO, NY); Güémez, alt. 600 m., *Runyon* 732 (US); river valley near Nogales, Jammave, *von Rozynski* 69 (F).

22. ARGEMONE **polyanthemos** (Fedde) G. B. Ownb., stat. nov.

A. intermedia var. *polyanthemos* Fedde, in Pflanzenr. 4 (104): 283. 1909; not *A. intermedia* Sweet.

A. alba James, Long's Exped. 1: 461. 1823; Gray, Syn. Fl. N. Am. 1 (1): 88. 1895, as to Nebraska distribution; Rydb., Fl. Black Hills, in Contr. U. S. Nat. Herb. 3: 483. 1896; Britton & Brown, Ill. Fl. 2: 101. 1897, as to Great Plains distribution; Stemen & Myers, Okla. Fl., p. 162. 1937; not *A. alba* Lestib; not *A. alba* Raf.

A. mexicana James, in Trans. Am. Phil. Soc., n.s., 2: 183. 1825; Torrey in Emory, Notes Mil. Rec. Ft. Leavenw. to San Diego, p. 406. 1848; Torrey, in Pac. R. Rep. 4 (5): 64. 1856; Port. & Coult., Syn. Fl. Colo., p. 6. 1874, in part; not *A. mexicana* L.

A. mexicana β *albiflora* Torrey, in Ann. Lyc. Nat. Hist. N. Y. 2: 166. 1828; Torrey, in Fremont, Rep., p. 87. 1845; Kuntze, Rev. Gen. 1: 12. 1891, as to Colorado distribution; not *A. mexicana* β *albiflora* DC.; not *A. mexicana* L.; not *A. albiflora* Hornem.

A. mexicana var. *albiflora* Gray, in Pac. R. Rep. 12 (2): 40. 1860; not *A. mexicana* L.; not *A. albiflora* Hornem.

A. hispida Hook., in Curtis's Bot. Mag. 104: t. 6402. 1878, as to plant figured; not *A. hispida* Gray.

A. platyceras Coult., Man., p. 13. 1885, in part; Fedde, in Pflanzenr. 4 (104): 283. 1909, in small part; Harrington, Man. Pl. Colo., p. 252. 1954, as to Wyoming, Colorado and Nebraska distributions; not *A. platyceras* L. & O.

A. albiflora Rydb., Fl. Sand Hills, in Contr. U. S. Nat. Herb. 3: 149. 1895; not *A. albiflora* Hornem.

A. intermedia var. *typica* Prain, in Journ. Bot. 33: 363. 1895, in part; not *A. intermedia* Sweet.

A. intermedia Eastwood, in Erythea 4: 96. 1896, as to Colorado distribution; Brit., Man., p. 439. 1901, as to Great Plains distribution; Nels., Analyt. Key Fl. Pl. Rocky Mt. Reg., p. 27. 1902; Small, Fl. s.e. U. S., p. 462. 1903, as to Great Plains distribution; Rydb., Fl. Colo., p. 149. 1906, excluding Mexico distributions; Robins. & Fern., Gray's Man., ed. 7, p. 416. 1908, excluding Illinois specimen; Coult. & Nels., New Man. Bot., p. 206. 1909; Fedde, in Pflanzenr. 4 (104): 281, in part, p. 274, fig. 36J, K. 1909; Nelson, Sp. Fl., p. 59. 1912; Britton & Brown, Ill. Fl., ed. 2, 2: 139. 1913, as to Great Plains distribution; Woot. & Standl., Fl. N. Mex., in Contr. U. S. Nat. Herb. 19: 261. 1915, as to New Mexico distribution; Rydb., Fl. R. Mts., p. 318. 1917, excluding Mexico and Utah distributions; Peters., Fl. Nebr., ed. 3, p. 67. 1923; Over, Fl. S. Dak.,

p. 50. 1932; Rydb., Fl. Pr. & Pl., p. 353. 1932, excluding Missouri and Mexico distributions; Stemen & Myers, Okla. Fl., p. 162. 1937; Gates, Fl. Kans., p. 156. 1940; Stevens, Kans. Wild Fl., p. 116. 1948; Fernald, Gray's Man., ed. 8, p. 681. 1950, excluding Illinois and Missouri distributions; Gleason, New Ill. Fl. 2: 199. 1952, as to Great Plains distribution; Weber, Handb. Pl. Colo. Fr. R., p. 106. 1953; Harringt., Man. Pl. Colo., p. 252. 1954, excluding Arizona distribution; not *A. intermedia* Sweet.

Annual or biennial with a deep tap root and bright yellow latex; stems 1-5, 4-8 (-12) dm. tall, cymosely branched, sparingly prickly with stout, perpendicular or recurved prickles; leaves glaucous, succulent, the lower ones oblanceolate, lobed to two-thirds the distance to the midrib, the lobes oblong, the middle and upper ones elliptic-ovate, more shallowly lobed, the uppermost definitely clasping the stem, the leaf surfaces with scattered, perpendicular or recurved prickles on the main veins below, totally smooth above; buds elliptic-oblong, the body 10-15 mm. broad, 15-22 mm. long, rather sparingly to moderately prickly with spreading prickles, the sepal horns essentially terete, 6-10 (-15) mm. long, usually completely devoid of prickles; flowers ordinarily 7-10 cm. in diameter, usually rather closely subtended by 1-2 foliar bracts, but sometimes the bracts distant; petals white, very rarely lavender, the inner broadly obovate-obcuneate, the outer suborbicular, the outer margins minutely erose; stamens numerous, 150 or more, the filaments lemon-yellow, the anthers bright yellow, equalling the stigma in length at anthesis; stigma purple, 3.0-4.5 mm. broad, 2.0-3.0 mm. high, 3-4-lobed; capsules 3-4-carpellate, narrowly to broadly elliptical, the width, exclusive of armature, 10-15 (-17) mm., the length, including the stigma, 35-50 (30-) mm., stoutly spinescent with widely spaced, spreading or recurved, simple spines, the largest of which are about 8-10 mm. long, these commonly interspersed with a few smaller ones, the capsular surface clearly visible; seeds about 2 mm. long. (Ill.: Fig. 23, 1-3; Dist.: Fig. 25.)

Holotype: *James Mooney s.n.*, collected on the Kiowa Reservation, Caddo Co., Oklahoma, Aug. 15, 1895 (US; isotype, F, fruits only).

Habitat and distribution: Prairies, foothills, and mesas, sandy or gravelly soils, roadsides, fields, pastures, waste ground; generally distributed from the eastern base of the Rocky Mountains across the plains from southwestern South Dakota, eastern Wyoming to New Mexico and Texas. Outlying localities are found in Montana, Utah (doubtless by introduction), western Colorado, southern New Mexico, and east-central Texas (doubtless by introduction). The species is found at elevations of less than 1000 ft. in eastern Kansas and Texas to over 7000 ft. in Colorado and New Mexico, but over most of its range it grows at elevations of 3000 to 6000 ft.

Flowering and fruiting dates: At lower elevations to the south flowering may begin by April 15, at higher elevations to the north it may be delayed to June 15 or later; flowering continues as local conditions permit through the summer; fruits begin to mature about a month after first flowering and continue to mature until late September or early October.

A. polyanthemos is distinguished by the sparingly prickly stems, the succulent, usually shallowly lobed leaves which are devoid of prickles on their upper surfaces, the upper ones usually clasping, and by the stoutly but usually distantly spinescent, elliptical capsules. The species is closely related to *A. albiflora* Hornem., and treated more conservatively, *A. poly-*

FIG. 23. *A. polyanthemos*. 1. Habit × 1. *Osterhout s.n.* (RM 31119). 2. Capsule × 1. Cult. from seeds of *Ownbey & Ownbey* 1323 (MIN). 3. Bud × 1. Same as 1.

anthemos would probably be made a subspecies of the latter. It differs from *A. albiflora* subsp. *albiflora*, however, in the narrowly elliptical rather than broadly oblong capsules, the usually longer and more numerous stamens, longer sepal horns, denser foliage and shorter stature. *A. polyanthemos* differs from *A. albiflora* subsp. *texana* in its ordinarily much less prickly capsules, less prickly stems, more glaucous leaves of thicker texture, and lower stature. It appears to hybridize with the latter subspecies in eastern Texas where *A. polyanthemos* is probably introduced and ephemeral in pure state. A fair percentage of specimens from this area can be placed only with reservations with either species. Also, there

appears to be some influence of *A. albiflora* subsp. *texana* on *A. polyanthemos* in northern Texas and adjacent Oklahoma but this influence grows less pronounced as the distance from the natural area of *A. albiflora* increases. This presumed introgression is evidenced by more prickly buds and capsules as well as by leaves of intermediate character in specimens of suspected hybrid ancestry.

It is regrettable that a new name must be introduced for the well-known plant of the western plains which for many decades has been called *A. intermedia* Sweet by American botanists. The exact identity of *A. intermedia* has yet to be determined, but it seems certain that it is not conspecific with *A. polyanthemos*. The former was described from plants grown from seeds from Mexico; the latter is not found outside the United States. The presence in Mexico of argemones which in the past have been lumped with *A. polyanthemos* under the binomial *A. intermedia*, even when the original application of *A. intermedia* was unclear has led to much confusion. The important fact to be emphasized here is that the name *A. intermedia* is a nomen confusum which cannot be applied to any species of *Argemone* with assurance. Even though its true identity may ultimately be determined the name cannot be applied, on distributional grounds, to the taxon native to the western Great Plains and foothills of the Rocky Mountains.

As originally proposed, *A. intermedia* var. *polyanthemos* Fedde was superfluous since the variety is indistinguishable from other specimens from the Great Plains cited by Fedde under *A. intermedia* proper. As a result of the rejection of the name *A. intermedia* for the Great Plains plant, however, Fedde's varietal epithet becomes available for the species. The application of the name is manifestly far broader than originally intended, but in this way the introduction of an entirely new name is avoided. Only one specimen is cited in the original description of var. *polyanthemos*, viz., *Mooney s.n.* from the Kiowa Reservation, Oklahoma, 1895. A specimen bearing these data and annotated by Fedde as his variety is deposited at the U. S. National Herbarium. Presumably this is the holotype.

Exactly which species of *Argemone* was introduced into England in 1828 and named *A. intermedia* by Sweet remains obscure. The species was not illustrated anywhere and as nearly as I can ascertain no specimens were preserved; at any rate no specimens from this period of authentic *A. intermedia* seem to be available at Kew. Prain makes no mention of any such specimens in any of the herbaria consulted in preparation of his revision, nor are his reasons for taking up the name clear. As is pointed out below *A. intermedia* var. *typica* of Prain contains many diverse elements which have in common white or pink petals and a paucity of spines on the foliage and stems. If one could overlook the stated geographical

origin of *A. intermedia* Sweet it is conceivable that it might really be conspecific with *A. polyanthemos*. There were certainly countless opportunities for the introduction of seeds from the United States prior to 1828.

Several taxa were included by Prain under *A. intermedia* var. *typica*. These are *A. corymbosa*, *A. gracilenta*, *A. polyanthemos* and *A. sanguinea*, as to specimens cited. Except for *A. corymbosa*, these were published subsequently to Prain's revision. His limited understanding of these taxa may unquestionably be ascribed to a deficiency of specimens in European herbaria. Under the circumstances, his reluctance to propose new names is commendable.

In Fedde's monograph, the typical element of *A. intermedia* is even more diverse, judging from the specimens cited. Elements of *A. albiflora* subsp. *texana*, *A. arida*, *A. grandiflora* subsp. *armata*, *A. munita* subsp. *munita*, *A. polyanthemos* and *A. sanguinea* are included. Fedde's treatment is an advance over that of Prain in that *A. corymbosa* is given varietal status and *A. gracilenta* is removed entirely from this complex. Some specimens of *A. polyanthemos* were also cited by Fedde under *A. platyceras*.

A species which without question is *A. polyanthemos* was introduced into Europe in 1877 by means of seeds collected by J. D. Hooker in Colorado. They were grown at Kew and figured in Curtis's Botanical Magazine in 1878 under the name *A. hispida* Gray. The plate excellently represents *A. polyanthemos* except for the stigma which is incorrectly drawn. In Hooker's discussion the species is confused with true *A. hispida* as might be expected, and with *A. munita*.

Prain erred in assigning his var. *stenopetala* to *A. intermedia* Sweet, a point of view subsequently adopted by Fedde. I have collected and studied this taxon in the field and am convinced that it is more closely allied to *A. ochroleuca* than to any of the white-flowered argemones. Rose, who was thoroughly familiar with Mexican *Argemone*, raised Prain's variety to species rank, certainly a more acceptable viewpoint. I choose to treat the taxon as a subspecies of *A. ochroleuca* for reasons discussed under that species.

A. alba James is validly although very casually published. It applies without doubt to the same taxon as *A. polyanthemos*. *A. alba* James is, fortunately, a later homonym of *A. alba* Raf. which in turn is a synonym of *A. albiflora* Hornem. We are thereby freed from any eventuality which might require the revival of *A. alba* James, a step which would unavoidably lead to confusion.

Specimens examined: UNITED STATES.

COLORADO

Boulder Co.: near Bounder, alt. 5000-6000 ft., *Tweedy* 4966 (NY, RM). Cheyenne Co.: 1.3 miles s. of Kit Carson, *Ownbey & Ownbey* 1703 (MIN). Clear Creek Co.: .2 mile w. of Dumont, *Ownbey & Ownbey* 1314 (COLO, MIN). Denver Co.: North Denver, *Eastwood* 39a (CAS, GH, MO, UC, US). Elbert Co.: 7 miles w. of Limon, *Ownbey* 1310 (GH, MO, NY, RM, UC). El Paso Co.: Manitou, alt. 2100 m., *Clements & Clements* 5 (DS, GH, MIN, MO, NY, RM, US). Jefferson Co.: 10 miles w. of Denver, *Nelson* 10953 (DS, MO, RM). Larimer Co.: about 20 miles n. of Ft. Collins, Hwy. 287, *Ownbey & Ownbey* 1311 (ARIZ, BM, CAS, COLO, GH, MIN, NEW MEX, RM); Ft. Collins, alt. 5500 ft., *Sheldon* 28 (F, NY, US). Las Animas Co.: Starkville, *Ownbey & Ownbey* 1486 (ARIZ, COLO, GH, MICH, MIN, RM); 2 miles w. of Carrizo Mt., *Rogers* 6192 (TEX). Lincoln Co.: 10.5 miles s.e. of Hugo, *Ownbey & Ownbey* 1701 (MIN). Montrose Co.: Black Canyon, region of Gunnison watershed, alt. 7075 ft., *Baker* 699 (GH, MIN, MO, ND, NY, POM, RM, UC, US). Pueblo Co.: Pueblo, *Woodward s.n.* (GH). Weld Co.: New Windsor, *Osterhout* 2317 (NY, RM, US); 3.2 miles s.w. of Roggen, Hwy. 6, *Ownbey & Ownbey* 1317 (COLO, MIN, UC, US).

KANSAS

Barton Co.: no locality, *Hitchcock s.n.* (KSC). Cheyenne Co.: no locality, *White s.n.* (KSC). Clark Co.: 8 miles s. of Sitka, *Rydberg & Imler* 1123 (KANU, NY). Edwards Co.: no locality, *Finch* 84 (KSC, MO). Elk Co.: no locality, *Clothier & Whitford s.n.* (KSC). Ellis Co.: no locality, *Zeller s.n.* (MO). Ford Co.: 3 miles s. of Dodge City, alt. 2480 ft., *Horr* 3425 (GH, KANU, TEX). Geary Co.: n. of Alida, *Gates* 21247 (MIN, RM). Gove Co.: no locality, *Hitchcock s.n.* (KSC). Greeley Co.: 14.4 miles s. of Tribune, *Ownbey & Ownbey* 1673 (ILL, KSC, MIN, RM, SMU). Kearney Co.: no locality, *Hitchcock s.n.* (KSC). Kiowa Co.: near Haviland, *Frame s.n.* (US). McPherson Co.: near Lindsborg, *Bodin s.n.* (MIN). Norton Co.: Norton, *Smyth* 37 (KSC, NY). Osborne Co.: Osborne City, *Shear* 77 (F, GH, NY, RM, US). Ottawa Co.: no locality, *Hitchcock s.n.* (KSC). Pratt Co.: Turkey Creek, *Norris s.n.* (MO). Reno Co.: Hutchinson, *Smyth* 32 (F, NY, US). Republic Co.: Scandia, *Thomas s.n.* (KSC). Riley Co.: no locality, *Norton* 12 (GH, KSC, MO, NY, RM, US). Rooks Co.: Rockport, *Bartholomew s.n.* (MO). Shawnee Co.: 7 miles e. of Topeka, alt. 875 ft., *Horr* E220 (CAS, KANU, MIN, RM, TEX, US). Sumner Co.: no locality, *Clothier & Whitford s.n.* (KSC). Thomas Co.: no locality, *Hitchcock s.n.* (KSC). Washington Co.: 1 mile and 2 miles w. of Washington, *Horr* 4628 (KANU). County Uncertain: Republ. Fork of Kansas, *Engelmann s.n.* (MO); n.w. Kansas, *Rusby s.n.* (US).

MONTANA

Dawson Co.: Riverside, *Seymour s.n.* (GH). Treasure Co.: Myers, *Barnhart* 218 (NY); Hysham, *Hiller s. n.* (MIN). Yellowstone Co.: Custer, *Blankinship s.n.* (ND). County Uncertain: Upper Yellowstone, *Havard s.n.* (US).

NEBRASKA

Cherry Co.: 10 miles s.e. of Valentine, *Ownbey & Ownbey* 1554 (MIN). Cheyenne Co.: Sidney, alt. 4090 ft., *Blackwood* 3500 (GH). Custer Co.: Callaway, *Bates s.n.* (GH). Dawes Co.: White River near Crawford, alt. 1200 m., *MacDougal* 117 (NY). Deuel Co.: no locality, *Rydberg s.n.* (US). Franklin Co.: Franklin, *Hapeman s.n.* (CAS, UC). Hooker Co.: near Mullen, *Rydberg* 1358, *in part* (US). Keith Co.: Ogallala, *Hapeman s.n.* (MIN). Knox Co.: Niobrara, *Clements* 2706 (GH, MIN, NY, US). Lincoln Co.: forks of Platte, *Engelmann s.n.* (MO); 7.9 miles n.w. of Gothenburg, Hwy. 30, *Ownbey & Ownbey* 1323 (BM, CAS, GH, MIN, NY, RM, SMU). Morrill Co.: Bayard, *Hapeman s.n.* (MO). Nuckolls Co.: no locality, *Hedgecock s.n.* (MO). Redwillow Co.: e. of McCook, *Mathias* 320 (MO, POM). Saunders Co.: Ashland, *Williams s.n.* (US).

Sheridan Co.: no locality, *Hatcher s.n.* (UC). Sioux Co.: no locality, *Kramer* 113 (MO). Thomas Co.: Dismal River s. of Thedford, *Rydberg* 1358, *in part* (NY, US). Webster Co.: Red Cloud, *Bates s.n.* (GH). County Uncertain: Bad Lands, *Hayden s.n.* (MO); South Fork, *Hayden s.n.* (MO).

New Mexico

Curry Co.: 18.5 miles n. of Clovis, *Ownbey & Ownbey* 1738 (GH, MIN, NEW MEX, NY, RM, UC). Dona Ana Co.: 6.4 miles n.e. of Organ, *Ownbey & Ownbey* 1756 (ARIZ, BM, CAS, COLO, F, GH, MICH, MIN, NEW MEX, NY, POM, RM, SMU, TEX, UC, UTC, US); Organ Mts., *Vasey s.n.* (F, US); Organ Mts., alt. 5000 ft., *Wooton* 147 (KSC, MIN, MO, ND, NY, POM, RM, US). San Miguel Co.: Las Vegas, alt. 1850 m., *Arsène* 18394 (US). Santa Fe Co.: Walnut Creek, *Fendler* 20 (MO); 6 miles s.e. of Santa Fe, Hwy. 285, *Ownbey & Ownbey* 1482 (ARIZ, CAS, COLO, MIN, NEW MEX, NY, RM, SMU); near Glorieta, alt. 7300 ft., *Standley* 5205 (GH, MO, NY, US). Union Co.: 3.5 miles s. of Clayton, *Ownbey & Ownbey* 1737 (MIN).

Oklahoma

Alfalfa Co.: Aline, *Stevens* 803 (DS, GH, MIN, MO, NY, SMU, US). Caddo Co.: Kiowa Reservation, *Mooney s.n.* (US, holotype of *A. intermedia* var. *polyanthemos* Fedde; isotype, F). Cleveland Co.: Norman, *Emig* 358 (MO). Comanche Co.: Fort Sill, *Clemens* 11588 (MO). Harmon Co.: Hollis, *Stevens* 1072 (GH, MIN). Kingfisher Co.: Huntsville, *Blankinship s.n.* (GH). Logan Co.: near Langston, *Myers s.n.* (MIN). McClain Co.: 2 miles s. of Purcell, *Stoul* 21 (RM). Marshall Co.: .5 mile w. of UOBS, *Riggs s.n.* (SMU). Oklahoma Co.: Oklahoma City, *Shimek s.n.* (F, MO). Payne Co.: 9 miles w. of Stillwater, *McAllister* 70 (CAS). Roger Mills Co.: Antelope Hills, *Goodman* 4331 (TEX). Tillman Co.: Frederick, *Duncan* 17 (MO). Woods Co.: no locality, *White s.n.* (RM). County Uncertain: Deer Creek, *Bigelow s.n.* (US); Indian Territory, *Palmer* 8 (US).

South Dakota

Bennett Co.: Martin, *Moore* 847 (MIN). Custer Co.: Buffalo Gap, *Hayward* 2563 (F, RM); Hermosa, alt. 3500 ft., *Rydberg* 511 (NY, US). Fall River Co.: near Hot Springs, *Palmer* 37449 (GH, MO). Meade Co.: Tilford, *McIntosh* 467 (RM). Mellette Co.: White River, *Wallace* 101 (NY). Pennington Co.: Rapid City, *Lee* 442 (RM). Washabaugh Co.: Bear Creek, *Visher* 2044 (F, NY).

Texas

Anderson Co.: Palestine, *Eggert s.n.* (MO). Archer Co.: 2 miles w. of Archer City, *Shinners* 18549 (SMU). Bell Co.: 3 miles n.w. of Temple, *Wolff* 909 (US). Burnet Co.: along Colorado River, *Wolff* 3224 (US). Callahan Co.: Baird, *Palmer* 13691 (MO). Childress Co.: 19 miles n. of Childress, *Whitehouse* 18705 (SMU). Clay Co.: 11.8 miles s. of Petrolia, Hwy. 148, *Whitehouse* 10835 (SMU). Collin Co.: 4 miles n. of Celina, *Timmons* 734 (NY). Dallas Co.: Dallas, *Hynes s.n.* (TEX). Fannin Co.: Bonham, *Milligan s.n.* (US). Fisher Co.: Grady, *Shepherd s.n.* (US). Hall Co.: Estelline, *Reverchon s.n.* (MO). Hemphill Co.: Canadian, *Condit s.n.* (UC). Hutchinson Co.: Fritch, *Shepard* 51 (TEX). Johnson Co.: 13.5 miles s.w. of Cleburne, *Shinners* 11267 (SMU). Lipscomb Co.: Lipscomb, *Howell* 25 (US). Lubbock Co.: Lubbock, *Studhalter* 1244 (US). McLennan Co.: n. of Lake Waco, *Smith* 42 (TEX). Mills Co.: Goldthwaite, *Morgan s.n.* (NY, TEX). Mitchell Co.: Colorado, *Hooks* 15269 (GH). Montgomery Co.: no locality, *Dixon* 495 (GH, NY). Nolan Co.: Sweetwater, *Stanfield* 4 (TEX). Palo Pinto Co.: Brazos, *Wadsworth s.n.* (TEX). Parker Co.: Millsap, *Wadsworth s.n.* (TEX). Potter Co.: Amarillo, *Reverchon s.n.* (MO). Randall Co.: Canyon, *Palmer* 14039 (MO, US). Tarrant Co.: Fort Worth, *Ruth s.n.* (US), Fort Worth, *Ruth s.n.* (NY); Fort Worth, *Ruth s.n.* (MO). Taylor Co.: Camp Barkeley, *Tolstead* 7136 (TEX, UC). Wheeler Co.: Shamrock, *Tharp* 4368 (TEX). Wilbarger

Co.: Vernon, *Reverchon* 3706 (MO). Williamson Co.: Brushy Creek, *Whitehouse* 18693 (SMU). Young Co.: 3 miles s.e. of Olney, *Cory* 13105 (GH).

Utah

Salt Lake Co.: 3 miles s. of Beck's Hot Springs, alt. 4250 ft., *Garrett* 8615 (UC).

Wyoming

Albany Co.: Halleck Canyon, *Nelson* 7424 (GH, MIN, MO, NY, POM, RM, US). Converse Co.: Red (i.e., Bed) Tick Creek, *Nelson* 5042 (MO, NY, RM). Goshen Co.: near Lingle, *Ownbey & Ownbey* 1303 (MIN, RM). Platte Co.: Badger, *Nelson* 2102 (GH, MO, NY, RM); 1.7 miles n. of Wheatland, *Ownbey & Ownbey* 1305 (GH, MIN, OKL, RM). Weston Co.: Newcastle, *Hayward* 2050 (F, RM).

State Uncertain

Fremont's Exped. to Calif., *Fremont s.n.* (GH).

23. Argemone albiflora Hornem., Hort. Hafn., p. 489. 1815.

Annual or biennial with a deep tap root and yellow latex; stems usually 1, 4-10 (-15) dm. tall, often much branched, sparsely to rather moderately prickly; leaves pale glaucous or greenish, the basal and lower cauline oblanceolate, lobed from one-half to four-fifths the distance to the midrib, the lobes oblong, the middle and upper ones more shallowly lobed, the broad bases of the uppermost clasping, the leaf margins with acute teeth, the leaf surfaces sparingly prickly on the main veins below, totally smooth or rarely with a few weak prickles on the main veins above; buds broadly elliptical to subspherical, the body 10-16 mm. broad, 12-18 mm. long, sparingly to rather closely prickly, the sepal horns terete, 3-6 (-10) mm. long, usually smooth; flowers 5-10 cm. in diameter, rather closely to quite distantly subtended by 1-2 foliar bracts; petals white (rarely lavender ?), the outer ones suborbicular, the inner ones obovate-obcuneate, minutely erose on the outer margin; stamens 150 or more, the filaments lemon-yellow, the anthers yellow, equal to or shorter than the pistil at anthesis; stigma purple, 2-4 mm. broad, 1.5-3.0 mm. high; style sometimes evident; capsules 4-5 (3-7) -carpellate, narrowly elliptical to oblong-elliptic or oblong, the width, exclusive of spines, 10-15 (-25) mm., the length, including the stigma, 20-40 (-45) mm., stoutly armed with even-sized spines to more closely armed with large spines interspersed with smaller, uneven-sized spines and prickles, the largest spines 6-10 (-12) mm. long, the capsular surface clearly visible or partially obscured; seeds about 1.6-2.0 mm. long.

Lectotype: A cultivated specimen from Hornemann's herbarium labeled *Argemone albiflora* Hornem. in his handwriting (C).

In J. W. Hornemann's listing of the plants in the Royal Botanic Garden of Copenhagen, *A. albiflora* is said to have been introduced in 1812, doubtless to this garden. The species had already been cultivated for some years in other European gardens under the name *A. alba*. Two specimens of *A. albiflora* which were almost certainly available to Hornemann when he described the species are preserved at the Botanical Museum of the University of Copenhagen. One of these specimens is from Hornemann's herbarium; the label is in his handwriting and bears the name *Argemone albiflora* Hornem. For these reasons I am designating this specimen the lectotype of the species. Unfortunately, the label bears no date or place of cultivation. The other specimen referred to is from the herbarium of Schumacker, is identified in the handwriting of Schumacker

as *Argemone albiflora,* bears the symbol denoting the Copenhagen Garden (Hortus Hafniensis) and the date 1814. There can be no reasonable doubt of the authenticity of these two specimens. The plants themselves are excellently preserved and can be identified without question as the species native to coastal southeastern United States.

A. albiflora has not been separated into two subspecies by any previous author, but the morphological differences between the two regional phases seem of sufficient value to require this treatment. On the other hand, there is little doubt that the two taxa should be included in the same species on the basis of what appears to be complete or nearly complete interfertility. Controlled experimental crosses made by myself indicate the presence of no important sterility barriers between the two.

In addition to the key differences between the two subspecies of *A. albiflora*, they also differ in the ordinarily more deeply cut basal leaves of subsp. *texana* and in the generally more prickly stems of subsp. *texana*. The sepal horns of subsp. *albiflora* are ordinarily shorter and broader, and the over-all prickliness of the buds somewhat less. No prickles have been detected on the upper surfaces of the leaves in subsp. *albiflora*, but they are fairly common in subsp. *texana*, though in the latter case only a very few are present.

Key to the subspecies:

1. Capsules oblong to oblong-elliptic, the spines stout, even-sized and widely spaced; coastal areas, N. Carolina to Florida and Mississippi; introduced northward . . . . . 23a. *A. albiflora* subsp. *albiflora*

1. Capsules usually narrowly elliptical, the widely spaced large spines interspersed with uneven-sized smaller spines and prickles; eastern Texas; introduced to the northeast . . . . . 23b. *A. albiflora* subsp. *texana*.

23a. Argemone albiflora Hornem. subsp. albiflora

A. albiflora Hornem., Hort. Hafn., p. 489. 1815; Sims, in Curtis's Bot. Mag. 49: t. 2342. 1822; Loud., Hort. Brit., p. 216. 1830; Otto & Dietr., in Allgem. Gartenzeit. 1: 300. 1833.

A. mexicana var β Lamarck, Encycl. Méth. 1: 247. 1783; not *A. mexicana* L.

A. alba Lestib., Bot. Belg., ed. 2, pt. 3, 2: 132. 1799, nomen nudum; Raf., Fl. Ludov., p. 83. 1817; Gray, Syn. Fl. N. Am. 1 (1): 88. 1895, as to south coast distribution; Britton & Brown, Ill. Fl. 2: 101. 1897, as to Florida distribution only; Britton, Man., p. 439. 1901, excluding Texas distribution; Mohr, Pl. Alab., in Contr. U. S. Nat. Herb. 6: 520. 1901, as to South Atlantic States only; Small, Fl. s.e. U. S., p. 462. 1903, in part; Robins. & Fern., Gray's Man., ed. 7, p. 416. 1908; Fedde, in Pflanzenr. 4 (104): 279, 274, fig. 36F, G. 1909, excluding Texas specimens; Britton & Brown, Ill. Fl., ed. 2, 2: 139. 1913, in part; Small, Fl. Flor. Keys, p. 52. 1913; Small, Man. s.e. Fl., p. 548. 1933, in part; Steyerm., Sp. Fl. Mo., p. 214. 1940, in part; Fernald, Gray's Man., ed. 8, p. 681. 1950; Gleason, New Ill. Fl. 2: 199. 1952, in part; Jones & Fuller, Vasc. Pl. Ill., p. 221. 1955; not *A. alba* Jones.

A. mexicana Pursh, Fl. Am. Sept. 2: 366. 1814, as to white-flowered variety; Elliott, Bot. Carol. & Georg. 2: 13. 1824, as to white-flowered variety; Beck, Botany, p. 21. 1833, in part; Gray, Man., ed. 1, p. 26. 1848, excluding yellow-flowered component;

Chapm., Fl. So. U. S., p. 21. 1860, as to white-flowered plants; Chapm., Fl. So. U. S., ed. 3, p. 20. 1897, as to white-flowered plants; not *A. mexicana* L.

Argemone, species with white flowers, Nutt., Gen. 2: 9. 1818.

A. mexicana β *albiflora* DC., Reg. Veg. Syst. Nat. 2: 86. 1821, as to Georgia and Louisiana distribution; DC., Prodr. 1: 120. 1824; Lindl., in Bot. Reg. 16: t. 1343. 1830, in synonymy; not *A. mexicana* L.

A. georgiana Croom, in Am. Journ. Sci. 25: 75. 1834.

A. mexicana var. γ Torr. & Gray, Fl. N. Am. 1: 61. 1838; Walp., Rep. 1: 109. 1842; not *A. mexicana* L.

A. vulgaris γ Spach, Hist. Nat. Vég. 7: 26. 1839.

A. alba var. *typica* Prain, in Journ. Bot. 33: 329. 1895, excluding Texas collection.

A. mexicana var. *alba* Chapm. ex Prain, l.c., p. 329. 1895, nomen nudum in synonomy; not *A. mexicana* L.

A. mexicana var. α Lamarck ex Prain, l.c., p. 329. 1895, in synonomy; not *A. mexicana* L.

A. intermedia Robins. & Fern., Gray's Man., ed. 7, p. 416. 1908, as to Illinois specimens; Fernald, Gray's Man., ed. 8, p. 681. 1950, as to Illinois and Missouri specimens, in part; Jones & Fuller, Vasc. Pl. Ill., p. 221. 1955; not *A. intermedia* Sweet.

Stems sparsely prickly with usually slender prickles; basal and lower cauline leaves lobed to about one-half to two-thirds the distance to the midrib, the middle and upper ones less deeply to shallowly lobed, the uppermost broadly ovate, the upper surfaces of the leaves totally smooth; buds subspherical, sparingly prickly with slender, spreading prickles, the sepal horns 3-5 mm. long, smooth; flowers often separated by an interval of 2-5 mm. from the nearest foliar bract, the interval often increasing to 1-several cm. during development of the fruit; petals white; stamens usually shorter than the pistil at anthesis; stigma 3-4 mm. broad, 2-3 mm. high; capsules 4-5 (3-7) -carpellate, typically oblong to oblong-elliptic, the width, exclusive of spines, 12-15 (-25) mm., the length, including the stigma, 20-40 (-45) mm., armed with widely spaced, stout, spreading, basally herbaceous, simple, mostly even-sized spines and occasionally with a very few smaller spines, the largest spines 6-8 (-10) mm. long, the capsular surface clearly visible; seeds about 2 mm. long. (Ill.: Fig. 24, 1-3; Dist.: Fig. 25.)

Lectotype: That of the species.

Habitat and distribution: In waste places, vacant lots, roadsides, beaches, dunes, in sandy soil. Possibly native only to northern Florida but now established along the coast from southeastern North Carolina across Florida to Mississippi. All records from northward and westward, e.g., Connecticut, Illinois, and Missouri, represent escapes from cultivation.

Flowering and fruiting dates: In Florida and adjacent coastal areas flowering begins in late March and continues through the summer as local conditions permit; first fruits are matured about May 1. When introduced farther north, flowering and fruiting dates are somewhat delayed.

A. albiflora subsp. *albiflora* is best distinguished on the basis of the usually oblong, 4-7-carpellate, stoutly but distantly spinescent capsules. Important supplementary characters are found in the sparsely prickly stems, the smooth upper surfaces of the leaves, the clasping upper leaves, the subspherical buds with short sepal horns and the stamens which are shorter than the ovary at anthesis. Occasionally buds with four sepals and eight petals are seen. Supernumerary sepals and petals are not rare

in *Argemone* and I do not ascribe any taxonomic importance to their occasional occurrence in *A. albiflora*. The tendency to develop a wide interval between the flower or capsule and the first foliar bract in *A. albiflora* has been stressed by previous authors. Again, I do not find this feature to be of particular taxonomic importance although undeniably true.

The natural distribution of *A. albiflora* subsp. *albiflora* is difficult to circumscribe due to the readiness by which it becomes established in unstable habitats in the south. It is a weed in every sense of the word on vacant lots and along roadways in coastal areas of the southeast. Having collected it at several stations in the southeast, the present writer has never seen it growing in indisputably natural circumstances, i.e. as an obvious component of a naturally occurring plant community. In my opinion this taxon represents a relict northern Florida subspecies which during rather recent times has spread along the coast both northward and westward as a ruderal weed. Probably it is not native to the Florida Keys.

The name taken up for this subspecies by Prain was *A. alba* Lestib., the oldest published binomial for the taxon. He points out that, at the time Lestibondois wrote, this was the only white-flowered *Argemone* known in Europe and that other white-flowered species were not introduced until 1827. *A. alba* Lestib. is, however, a nomen nudum and in accordance with the International Rules the name must be abandoned in favor of the first validly published binomial. The history of the origin of the name *A. alba* as narrated by Prain is of much interest.

Since *A. alba* Lestib. is a nomen nudum it has no taxonomic standing under the Rules and the epithet *alba* is available for this or any other species of *Argemone*. The epithet was, however, next applied to what is almost certainly the same taxon, *A. alba* Rafinesque, and was validly published by him. The valid publication of *A. alba* Raf. is, however, antedated by valid publication of *A. albiflora* Hornem. for the same taxon. *A. alba* James, published in 1823, is a synonym of *A. polyanthemos* (Fedde) Ownbey, and a later homonym of *A. albiflora* Hornem.

As understood by Prain, *A. alba* (i.e., *A albiflora*) consisted of two varieties, var. *typica* and var. *glauca*. My two subspecies of *A. albiflora* are equivalent to Prain's var. *typica*. Subsp. *albiflora* includes the classical material of this taxon. Prain's var. *glauca* (i.e., *A. glauca* Nutt., MSS), endemic to the Hawaiian Islands, is a distinct species whose closest affinities certainly do not lie with any North American species of *Argemone*.

I have seen no specimens purported to be *A. alba* Raf. The description could certainly appertain to *A. albiflora* Hornem. If this is true, then its introduction into Louisiana could not have been from Mexico as is stated by Rafinesque. Probably it came from Florida. In reaching this conclusion, I differ from Prain (1895, p. 330), who does not question the

FIG. 24. 1-3. *A. albiflora* subsp. *albiflora*. 1. Bud × 1. Cult. from seeds of *Ownbey & Ownbey* 1350 (MIN). 2. Middle cauline leaf, under surface × ½. Cult. from seeds of *Ownbey & Ownbey* 1375 (MIN). 3. Capsule × 1. Same as 1. 4-6. *A. albiflora* subsp. *texana*. 4. Habit × ½. Holotype, *Ownbey & Ownbey* 1388 (MIN). 5. Bud × 1. Cult. from seeds of *Ownbey & Ownbey* 1387 (MIN). 6. Capsule × 1. Same as 5.

accuracy of Rafinesque's statement as to the origin of the Louisiana plants. Rafinesque's description reads: "Caule foliisque spinosis, foliis runcinatis, capsulis oblongis pentagonis spinosis semi-5-valvis." Only one white-flowered Mexican species of *Argemone* has capsules of this description. This is *A. grandiflora* which, except for the newly described subsp. *armata*, has essentially unarmed stems and must be eliminated from consideration for this and other reasons.

Specimens examined: UNITED STATES.

ALABAMA

Macon Co.: Tuskegee, *Andrews s.n.* (NY, US).

CONNECTICUT

Fairfield Co.: Fairfield, *Eames* 11901a (US).

FLORIDA

Bay Co.: Panama City, *Ownbey & Ownbey* 1377 (MICH, MIN). Columbia Co.: Lake City, *Rolfs* 101 (GH, MIN, RM). Duval Co.: Pilot Island, mouth of St. John's River, *Small & DeWinkeler* 9838 (NY, US). Franklin Co.: Carrabelle, *Ownbey & Ownbey* 1375 (DUKE, GA, GH, MIN, NCU, TEX, US). Lake Co.: Eustis, *Nash* 656 (F, GH, MIN, MO, ND, NY, UC, US). Monroe Co.: Key West, *Blodgett s.n.* (NY); Indian Key, *Blodgett s.n.* (NY). Leon Co.: near Tallahassee, *Berg s.n.* (NY). Pinellas Co.: Palm Harbor, *Moldenke* 1059 (MO, NY). Putnam Co.: Palatka, *ex herb. Hood s.n.* (MO).

GEORGIA

Chatham Co.: Savanna, *Ownbey & Ownbey* 1350 (C, CAS, F, GA, GH, K, KSC, MIN, NY, RM, SMU, TEX, UC, US). McIntosh Co.: .5 miles s. of Darien, *Ownbey & Ownbey* 1352 (DUKE, GA, MIN, NCU, SMU). Glynn Co.: Ocean Pier, St. Simon's Island, *Harper* 1530 (GH, MO, NY, US).

ILLINOIS

Henderson Co.: Oquawka, *Patterson s.n.* (F, MO). Madison Co.: Pope Station, *Eggert s.n.* (MIN, MO, UC). Morgan Co.: banks of Illinois River, Meredosia, *Seymour s.n.* (GH). Peoria Co.: Peoria, *McDonald s.n.* (GH). Stephenson Co.: Freeport, *Johnson s.n.* (US).

MISSISSIPPI

Hancock Co.: Bay of St. Louis, *Cook s.n.* (US). Harrison Co.: 4.5 miles e. of Gulfport, *Ownbey & Ownbey* 1379 (GA, MIN, NCU, SMU); Biloxi, *Tracy* 6894 (F, GH, MIN, MO, NY, US).

MISSOURI

Dunklin Co.: Campbell, *Bush* 3 (MO, NY). Howell Co.: Carson, *Eggert s.n.* (MO). Jackson Co.: Sheffield, *Bush* 9480 (F, MO). St. Louis Co.: Allenton, *Letterman s.n.* (MO).

NORTH CAROLINA

Brunswick Co.: Southport, *Godfrey & Wiebe* 50378 (GH, SMU).

SOUTH CAROLINA

Beaufort Co.: Beaufort, *Churchill s.n.* (CAS, GH, MO). Charleston Co.: Sullivans Island, *Palmer s.n.* (US). Jasper Co.: no locality, *Meyers s.n.* (NY).

23b. ARGEMONE ALBIFLORA Hornem. subsp. **texana** G. B. Ownb., subsp. nov.

A. alba Gray, Syn. Fl. N. Am. I (1): 88. 1895, as to Texas distribution, in part; Britton, Man., p. 439. 1901, as to Texas distribution; Small, Fl. s.e. U. S., p. 462. 1903, in part; Fedde, in Pflanzenr. 4 (104): 279. 1909, as to *Rose* 4893 cited; Britton & Brown, Ill. Fl., ed. 2, 2: 139. 1913, in part; Small, Man. s.e. Fl., p. 548. 1933, in part; Steyerm., Sp. Fl. Mo., p. 214, Pl. 57, fig. 3. 1940, in part; Gleason, New Ill. Fl. 2: 199. 1952, in part; not *A. alba* Lestib.

A. intermedia Fedde, in Pflanzenr. 4 (104): 281. 1909, in small part; Fernald, Gray's Man., ed. 8, p. 681. 1950, as to Missouri specimens, in part; not *A. intermedia* Sweet.

A. platyceras Fedde, in Pflanzenr. 4 (104): 283. 1909, in small part; not *A. platyceras* L. & O.

Herba annua aut biennis latice flavo. Caules 4-10 (-15) dm. alti, sparse vel moderate aculeati. Folia inferiora saepe pinnatifida lobis oblongis, superiora levitius lobata, terminalia caulem ad basem latam amplectentia. Lamina subter in venis principalibus sparse aculeata, supra omnino inermia aut subinermia. Alabastra late elliptica vel subsphaerica. Sepalorum cornua subteretia, 4-6 (-10) mm. longa. Flores 5-10 cm. diametro, petalis albis, staminibus circa 150 vel plus. Capsulae 4-5 (3-5) -carpellatae, anguste ellipticae, 10-14 mm. latae, 25-35 (-40) mm. longae, moderate spinescentes aut spinis plerumque tenuibus patentibus basaliter herbaceis simplicibus aut multis et inaequalibus et parvioribus spinis et quoque aculeis. Semina circa 1.7 mm. longa.

Stems sparsely to rather moderately prickly with usually slender, perpendicular or recurved prickles; basal and lower cauline leaves often lobed to near the midrib, the middle and upper ones more shallowly lobed, the upper surfaces of the leaves either totally smooth or with a very few weak prickles mainly on the midrib; buds broadly elliptical to subspherical, sparingly to rather closely prickly with slender, spreading, simple prickles, the sepal horns 4-6 (-10) mm. long, smooth or sparingly prickly at the base; flowers usually rather closely subtended by 1-2 foliar bracts, the interval between flower and nearest bract sometimes to about 5 mm. at fruiting time; petals white (or rarely lavender ?); stamens equal to or shorter than the pistil at anthesis; stigma 2.0-3.5 mm. broad, 1.5-2.0 mm. high; style sometimes evident; capsules 4-5 (3-) -carpellate, typically narrowly elliptical, the width, exclusive of spines, 10-14 mm., the length, including the stigma, 25-35 (-40) mm., moderately armed with usually slender, spreading, basally herbaceous, simple spines as well as numerous uneven-sized smaller spines and prickles, the largest spines 7-10 (-12) mm. long, the capsular surface partially obscured; seeds about 1.7 mm. long. (Ill.: Fig. 24, 4-6; Dist.: Fig. 25.)

Holotype: *Gerald B. Ownbey & Findley Ownbey* 1388, from 4.3 miles w. of Brenham, Washington Co., Texas, July 11, 1950 (MIN; isotypes, GH, MIN, NY, SMU, UC, US).

Habitat and distribution: Sandy or gravelly soils, embankments, vacant lots, pastures, waste ground, roadsides, fence rows, railroad rights-of-way, abandoned fields, flat terrain or rolling hills, now usually a weed; probably originally of rather restricted range in eastern Texas, but now spread to northeastern Texas, northern Arkansas and southern Missouri.

Flowering and fruiting dates: Earliest flowers are produced about March 15 and flowering continues through spring, summer and fall if local conditions permit; first fruits may mature during the fourth week in April but fruits mature most abundantly during May and June; late fruits mature until October.

This subspecies is most readily distinguished by the narrowly elliptical capsules armed with larger spines intermingled with smaller, uneven-sized spines and prickles. Important supplementary characters are the deeply pinnatifid basal and lower cauline leaves, the clasping upper cauline leaves, the usually entirely smooth upper surfaces of the leaves, and the stamens which are often shorter than the pistil at anthesis.

The first specimens of this subspecies apparently were collected by Drummond in 1835. It has since been collected by many botanists, usually as single specimens. I have, however, thought it best to designate one of my own specimens as the holotype because of the opportunity thus afforded to distribute isotype material to a large number of institutions.

In southern Texas where the distributions of *A. albiflora* subsp. *texana* and *A. sanguinea* impinge upon each other, separation of immature material of the two is sometimes difficult. In most cases, the larger buds, flowers and stigmas of the latter species as well as the usually longer sepal horns serve to distinguish it, but all of these characters break down at times. The foliage of both taxa is highly variable and no constant differences have been found. Also, the petals in *A. sanguinea* although often lavender are sometimes white as in *A. albiflora*. Good differences between the two, however, do reside in the mature fruits in most instances.

There is unlimited opportunity for natural hybridization between *A. albiflora* subsp. *texana* and *A. sanguinea*. As far as is known, however, the former is always diploid and the latter always tetraploid in the distributional area common to both. If hybridization actually takes place it is doubtful if it proceeds beyond the first generation. The occurrence of even occasional hybrid plants would, nevertheless, account for some of the difficulties sometimes met with in distingnishing the two described above.

A. albiflora subsp. *texana* is thought to hybridize readily with *A. polyanthemos* in nature. A fuller discussion of this subject is presented under the latter species. The assumption is borne out by controlled crosses between cultivated plants of the two taxa which indicate that they may be crossed without great difficulty. A close genetic relationship is unquestionably present. The two taxa are sufficiently distinct on morphological and distributional grounds, however, to justify their recognition as separate species.

Specimens examined: UNITED STATES.

ARKANSAS

Clay Co.: Corning, *Eggert s.n.* (MO). Izard Co.: Guion, *Emig* 49 (MO). Marion Co.: Yellville, *Moore* 32662 (TEX). Stone Co.: Onia, alt. 750 ft., *Demaree* 27870 (RM).

MISSOURI

Butler Co.: Poplar Bluff, *Dewart s.n.* (MO); Neelyville, *Kellogg* 15186 (MO).

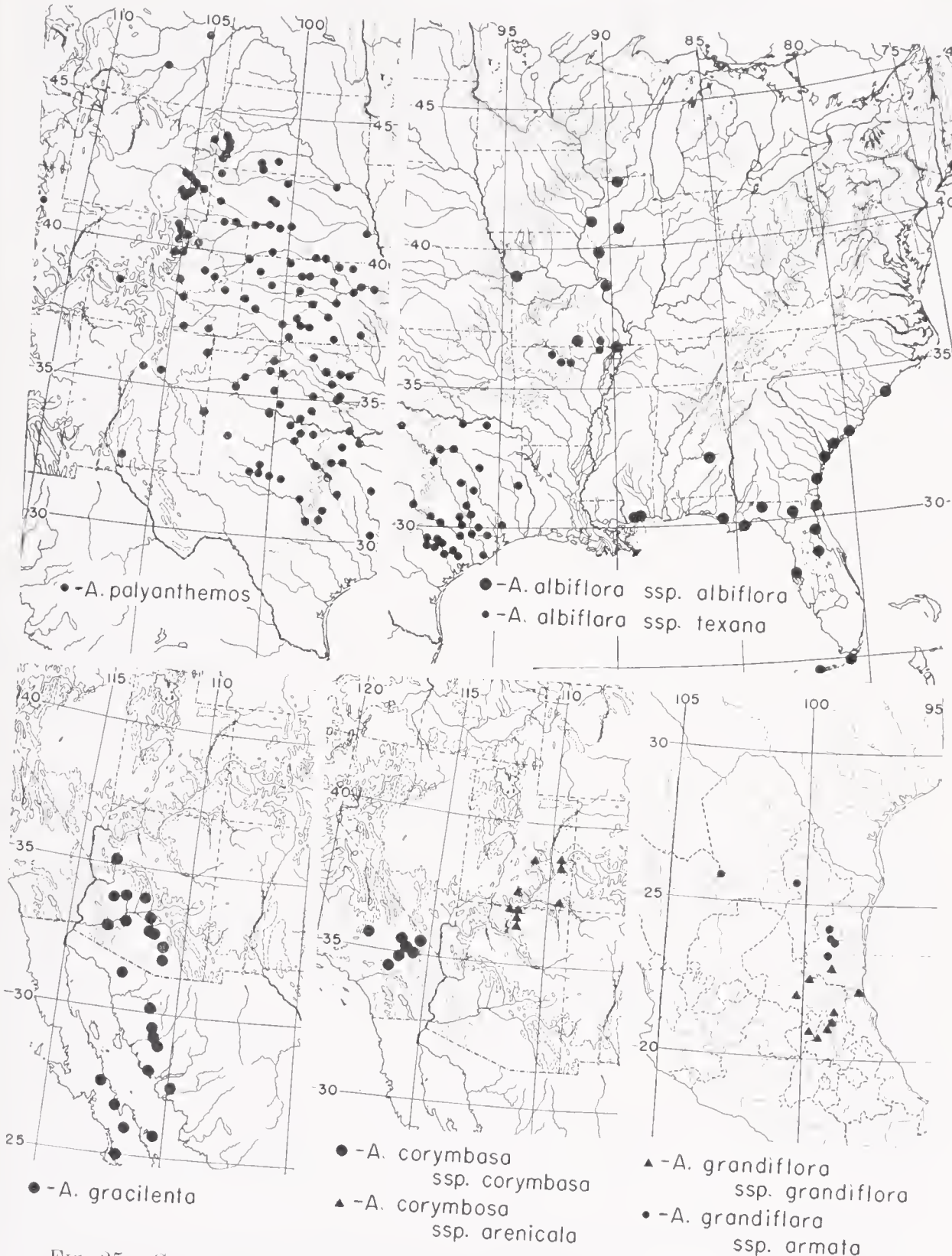

FIG. 25. Geographical distributions of species and subspecies as indicated.

TEXAS

Austin Co.: San Felipe, *Lindheimer s.n.* (MO); 8 miles e. of Sealy, *Cory* 55067 (SMU, US). Bastrop Co.: 7.9 miles w. of Bastrop, *Ownbey & Ownbey* 1393 (MIN, NCU, NY, SMU). Baylor Co.: w. of Seymour, *Shinners* 18596 (SMU). Brazoria Co.: Brazoria, *Palmer* 5123 (MO, POM, US). Brazos Co.: College Station, *Pammel s.n.* (MO). Burleson Co.: 2 miles s. of Somerville, *Shinners* 14683 (SMU). Caldwell Co.: no locality, *McBryce s.n.* (TEX). Colorado Co.: ¾ mile n.w. of Columbus, *Cory* 54272 (SMU). Dallas Co.: n.w. of Carrollton, .5 mile s.e. of Denton Co. line, *Shinners* 8509 (GH, SMU); no locality, *Reverchon s.n.* (MO). DeWitt Co.: Cuero, *Marlatt s.n.* (US). Fayette Co.: Schulenburg, *Ownbey & Ownbey* 1650 (C, CAS, F, GH, K, KSC, MICH, MIN, NCU, NY, RM, TEX, UC, US). Fort Bend Co.: 1.4 miles n.e. of Richmond bridge, *Ownbey & Ownbey* 1589 (MIN). Gonzales Co.: s.e. of Gonzales, *Whitehouse* 11806 (SMU). Grayson Co.: Denison, *Gentry* 303 (TEX). Guadalupe Co.: 3 miles s. of Seguin, *Cory* 54060 (SMU). Harris Co.: Houston, *Fisher* 306 (RM, US). Henderson Co.: Athens, *Shinners* 15115 (SMU). Jackson Co.: Horseshoe Lake, *Drushel* 6493 (MO). Lamar Co.: Paris, *McMullen s.n.* (TEX). Lavaca Co.: about 18 miles s.e. of Yoakum, *Tharp, Rogers & York* 49169 (TEX). Leon Co.: Normangee State Park, *Whitehouse* 11801 (SMU). Liberty Co.: near Liberty, *Rose* 4893 (US). Llano Co.: near Enchanted Rock, *Innes & Warnock* 786 (GH, TEX). Limestone Co.: 7.6 miles s.-s.w. of Mexia, *Shinners* 14549 (MIN, SMU). San Augustine Co.: San Augustine, *Crocket s.n.* (US). Somervell Co.: 4 miles n.e. of Glen Rose, *Wagner* 61 (SMU). Tarrant Co.: along T. & P. R.R., *Ruth s.n.* (F). Travis Co.: Austin, *Tharp s.n.* (GH, MO, UC). Waller Co.: 4.3 miles e. of Hempstead, *Ownbey & Ownbey* 1387 (DUKE, GA, MIN, TEX). Washington Co.: 4.3 miles w. of Brenham, *Ownbey & Ownbey* 1388 (MIN, holotype of *A. albiflora* subsp. *texana* Ownb.; isotypes, GH, MIN, NY, SMU, UC, US). Wilson Co.: Stockdale, *Cory* 54071 (SMU). County uncertain: no locality, *Drummond* 8 (GH); vicinity of Brazos, *Lindheimer s.n.* (MO).

Excluded Names

Argemone armeniaca L., Sp. Pl. 1: 509. 1753; Willd., Sp. Pl. 2: 1149. 1799; is *Papaver* sp.

Argemone cambrica (L.) Desportes, in Diet. Sci. Nat. 2: 481. 1804, is *Meconopsis cambrica* (L.) Vig.

Argemone intermedia Sweet, Hort. Brit., ed. 2, p. 585. 1830; Sweet, Hort. Brit., ed. 3, p. 22. 1839, of uncertain application. See discussion under *A. polyanthemos*.

Argemone pyrenaica L., Sp. Pl. 1: 509. 1753; Willd., Sp. Pl. 2: 1149. 1799; is *Papaver* sp.

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Rydberg, Per Axel. The North American species of Physalis and related genera. Vol. 4, No. 5. 78 p. 15 September 1896. $0.75.

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NEW YORK
BOTANICAL
GARDEN

Memoirs
of
The Torrey Botanical Club

Vol. 21, No. 2 May 26, 1960

Editor
MURRAY F. BUELL

A STUDY OF RUSSULA TYPES

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Published for the Club by
THE SEEMAN PRINTERY
Durham, N. C.

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A STUDY OF RUSSULA TYPES[1]

L. R. Hesler

In my effort better to understand the species of *Russula*, a study of certain North American types has been undertaken. Special attention has been given in these studies to the structure of the pileus cuticle, and to the ornamentation of the spores.

Studies of this kind have been reported by Singer, Burlingham, Schaeffer, Smith, and others (see Literature Cited), but in papers published to date, illustrations of the cuticle and spores have been limited or lacking.

In this paper is presented a series of illustrations of the spores and of the pileus cuticle-structures of one hundred fifty-nine species of *Russula* types and authentic collections.

Acknowledgment is made to the National Science Foundation for a grant supporting these studies, and to the following institutions for the loan of types: Harvard University, New York Botanical Garden, New York State Museum, The University of Florida, and The University of Michigan. The original drawings were made by the author. The plates were then prepared by Mrs. Romance F. Carrier, a former graduate student in botany at The University of Tennessee.

The Cuticle of the Pileus

The taxonomic value of the cuticle-structure in the genus *Russula* lies in its diversity. A tangential section through the pileus reveals that the cuticle-composition is of one of two general types: the cuticle may consist of an undifferentiated layer of hyphae which are repent, or ascendant (as in Figs. 179, 259, and others); or it may be differentiated into an outer layer,—the epicutis, and a subjacent zone,—the hypodermium (subcutis of some authors). There may be still a third zone, or layer, the subhypodermium, which is usually a conspicuous zone of parallel to interwoven hyphae disposed tangentially (Fig. 186a). The hypodermium is either pseudoparenchymatous (Figs. 195, 196, and others) or prosenchymatous (Fig. 186a, and many others) in structure and composition.

The composition of the epicutis is likewise diverse. It is composed of more or less erect hyphal elements which may be either septate (as in Figs. 185, 203) or non-septate (many instances). The free ends of the epicuticular hyphae may be either rounded or acute. These erect elements may be scattered over the surface, or they may be closely parallel, and thus may

[1] Contributions from the Botanical Laboratory, The University of Tennessee, N. Ser. No. 210.

form an hymeniform layer, or turf-like palisade. In a majority of the types studied, pilocystidia stand among the epicuticular hyphae (Figs. 160-165 and many others). These bodies are more or less clavate, broader than the hyphae, and usually with granular to banded contents.

Ornamentation of the Spores

In addition to spore form and size and the color of spore-deposits, the nature of spore-wall ornamentation is of specific taxonomic value. To study these ornamentations, spores from deposits, when available, or from the lamellae, are mounted in Melzer's reagent. In such mounts the ornamentations (warts, lines, bands) are stained dark-blue to blackish.

In the genus, spore ornamentations vary from minute punctations to conspicuous warts. In the spores of some species the warts are very short (0.1 μ or less), or in others they may be long (1.0-2.0 μ or more in height). The warts may be slender and acute, or broad and blunt. At times the warts are connected by fine lines, which in some species form a net-work, or the warts may be catenulate. In many species rather broad bands or ridges are present, and, with or without fine lines, may be disposed to form a reticulum.

Pleurocystidia and Cheilocystidia

Included in this treatise are several *Russula* types on which no studies up to this time have been reported. For these species, observations on pleurocystidia and cheilocystidia are recorded. For information on the cystidia of other *Russula* types, the reader is referred to the literature.

Explanation of Plates and Figures

In all drawings, the elements of the epicutis are reproduced at a magnification of 500; the spore-drawings are at a magnification of 1500. All structures were studied under an oil-immersion lens at a magnification of 1150.

Types Studied

In the descriptive legends, the *Russula* species studied are arranged alphabetically, and citation for each is given to the orginial description. Reference is also made to the accompanying figures which illustrate the structures. Finally, where Singer has published studies on the type, his publication is cited. Although most of the studies reported below are based on type-collections, some exceptions are noted.

R. admirabilis Beards. & Burl., Mycologia 31: 492. 1939. *Spores* (Fig. 6) 7.5-10 × 5.7-7 μ, warts 0.4-0.8 μ high, isolated or catenulate, at times with connecting fine lines. *Epicutis* (Fig. 271) composed of loosely interwoven hyphae, some with acute apices; some erect, others repent. *Pilocystidia* granular to banded, at times septate. (Singer 1957: 261.)

R. affinis Burl., Mycologia 16: 22. 1924. *Spores* (Fig. 2) 7-8 × 6-7 μ, warts 0.1 μ or less in height, isolated or with a few fine lines. *Epicutis* (Fig. 185) composed of tufts of pale brownish, septate, somewhat constricted hyphae, the apices more or less acute; with scattered, fusoid, granular to banded *pilocystidia*. (Singer 1939: 323.)

R. alachuana Murr., Mycologia 30: 362. 1943. *Spores* (Fig. 23) 7-9 × 6.5-8 μ, warts 0.4-1.0 μ high, ridges and a few fine lines forming a reticulum. *Epicutis* (Fig. 184) composed of constricted hyphae, each with a basal cell, the hyphae tending to form a palisade. *Pilocystidia* none. (Singer 1957: 182.)

R. albella Pk., New York State Mus. Ann. Rept. 50: 101. 1897. *Spores* (Fig. 69) 8-9 × 6.5-7.5 μ, warts 0.5-0.8 μ high, with some bands and fine lines. *Epicutis* (Fig. 186) at first composed of loosely interwoven, slender hyphae and clavate *pilocystidia*, some of which are buried, others protruding; in age, much of the original epicutis sloughs away, and is replaced by erect, constricted, broader, septate hyphae, without *pilocystidia*. (Singer 1943: 146.)

R. albiclavipes Murr., Lloydia 8: 263. 1945. *Spores* (Fig. 14) 9-11 × 8-9 μ, warts 0.8-1.4 μ high, isolated, or a few catenulate, rarely with fine lines which are indistinct. *Pleurocystidia* 52-65 × 6-8 μ, projecting 20-35 μ, fusoid to ventricose, empty, granular, or banded, apices acute, mucronate, or capitate; *cheilocystidia* 34-42 × 5-7 μ, ventricose, mucronate to appendiculate, empty, granular, to slightly banded. *Epicutis* (Fig. 201) composed of erect to ascendant, slightly constricted hyphae, with numerous long, banded *pilocystidia*. (No studies reported by Singer.)

R. albida Pk., New York State Mus. Bull. 1 (No. 2): 10. 1887. *Spores* (Fig. 96) 8-10 × 7.5-9 μ, warts 0.5-0.8 μ high, isolated or with short ridges and some fine lines. *Epicutis* (Fig. 198) composed of erect, versiform hyphal cells which arise from a bed of pseudoparenchyma; *pilocystidia* none. (Singer 1947: 180 does not mention the pseudoparenchymatous hypodermium.)

R. albidicremea Murr., Elisha Mitchell Sci. Soc. Jour. 55: 369. 1939. *Spores* (Fig. 57) 6.5-8 × 5.7-7 μ, warts 0.3-0.5 μ high, isolated, or with long, prominent bands, fine lines rare. *Pleurocystidia* 40-58 × 6-8 μ, scattered, often inconspicuous, ventricose to subcylindric, apices tapering or appendiculate, empty, granular, or banded: *cheilocystidia* 38-46 × 4-10 μ, ventricose to cylindric, apices tapering or mucronate, empty or banded. *Epicutis* (Fig. 200) composed of scattered to moderately dense, erect or ascendant hyphae, some slightly nodulose-constricted, tending to form a turf; *pilocystidia* none. (No studies reported by Singer.)

R. albidula Pk., Torrey Bot. Club Bull. 25: 370. 1898. The type could not be located. The following notes are based on my observations of a specimen, from Albany, collected by Beardslee at Asheville, North Carolina, 1917: *Spores* (Fig. 97) 7-8.5 × 5.5-7 μ, warts 0.2-0.5 μ high, at times catenulate, with some fine lines. *Pleurocystidia* 46-88 × 6-12 μ, fusoid, apices rounded, mucronate, or appendiculate, granular or banded; *cheilocystidia* 43-55 × 5-7 μ, fusoid, empty, granular, or banded. *Epicutis* (Fig. 274) composed of slender, loosely interwoven hyphae, erect or ascendant;

with slender, clavate *pilocystidia* which are granular to banded, occasionally septate. (No studies reported by Singer.)

R. albiduliformis Murr., Lloydia 6: 209. 1943. *Spores* (Fig. 26) mostly 5-6.5 × 4-5 μ, some 7-9.5 × 5-6.5 μ, warts 0.1 μ or less (rarely 0.2 μ) in height, with fine lines which are usually indistinct. *Epicutis* (Fig. 252) composed of cylindric, ventricose, nodulose, or even subulate hyphae, tending to occur at intervals in tufts as a turf; no *pilocystidia*. (Singer 1957: 178.)

R. albiflavescens Murr., Torrey Bot. Club Bull. 66: 154. 1939. The type was not located. The following notes are based on a specimen, No. F 10052, collected and determined by Murrill: *Spores* (Fig. 13) 9-11 × 7-8.5 μ, warts 0.6-1.0 μ high, isolated or with bands, without fine lines. *Pleurocystidia* numerous, 52-105 × 8-18 μ, ventricose to clavate, apices more or less acute, often with an exudate, banded; *cheilocystidia* 36-63 × 6-11 μ, clavate to subfusoid, empty or banded. *Epicutis* (Fig. 295) not differentiated; the cuticle composed mostly of repent hyphae, but with a few erect hyphae; no *pilocystidia*. (No studies reported by Singer.)

R. albimarginata Murr., Lloydia 7: 309. 1944. *Spores* (Fig. 149) 7-9 × 6-8 μ, warts 0.6-0.8 μ high, some catenulate, with some fine lines forming an incomplete reticulum. *Pleurocystidia* 48-71 × 4-8 μ, clavate, capitate to acutely mucronate, more or less banded; *cheilocystidia* 32-50 × 4-6 μ, fusoid to subclavate, mucronate, granular to banded. *Epicutis* (Fig. 300) composed of slender (2-2.5 μ broad) hyphae, with numerous granular *pilocystidia*, in each the apical portion often flask-shaped, and all forming a turf. (No studies reported by Singer.)

R. alutaceiformis Murr., Lloydia 6: 210. 1943. *Spores* (Fig. 43) 7.5-8.5 × 5.5-7 μ, warts 0.5-0.9 μ high, with short bands and fine lines forming a limited reticulum. *Pleurocystidia* 43-96 × 7-9 μ, fusoid to clavate, usually mucronate, empty or banded; *cheilocystidia* 30-50 × 6-8 μ, fusoid to clavate, mucronate or subcapitate, empty or banded. *Epicutis* (Fig. 299) composed of slender, erect hyphae, and with numerous clavate, granular to banded *pilocystidia*. (No studies reported by Singer.)

R. amygdaloides Kauff., Agar. Mich. 1: 162. 1918. *Spores* (Fig. 45) 8-10.5 × 7-9.5 μ, warts 0.7-1.2 μ high, some isolated, some catenulate, with a few fine lines. *Epicutis* (Fig. 235) composed of a palisade of hyphae which are irregularly constricted; no *pilocystidia*. (Singer 1957: 258.)

R. anisata Murr., Lloydia 7: 310. 1944. *Spores* (Fig. 114) 8-9 (10) × 6-6.5 μ, warts 0.4-0.6 μ high, some isolated, some catenulate, with a few indistinct fine lines which may not reach another wart. *Pleurocystidia* 41-56 × 4-8 μ, ventricose, more or less appendiculate, few, often inconspicuous, banded, granular, or empty; *cheilocystidia* 37-40 × 4-6 μ, few, ventricose, appendiculate, banded or empty. *Epicutis* (Fig. 193) of slender (0.5-1.0 μ, rarely 2 μ, broad), erect or ascendant hyphae, with conspicuous, irregularly constricted, at times septate *pilocystidia*. (No studies reported by Singer.)

R. anomala Pk., New York State Mus. Ann. Rept. 50: 99. 1898. *Spores* (Fig. 36) 9-10 × 7-8.5 μ, warts 0.7-1.3 μ high, some isolated, and some with a few fine lines and broad bands. *Epicutis* (Fig. 251) composed of erect to ascendant hypae which may be nodulose-constricted, apices rounded,

capitate, or acute; with numerous banded *pilocystidia*. (Singer 1943: 145 and 1947: 174-175 states that *R. subalbidula* Murr. is a synonym of *R. anomala* Pk.)

R. appalachiensis Singer, Sydowia 2: 39. 1948. *Spores* (Fig. 27) 7.5-10 × 5.5-7.5 μ, warts 0.3-0.7 μ high, isolated or with indistinct fine lines. *Epicutis* (Fig. 290) composed of versiform hyphae—cylindric, constricted-nodulose, with apices rounded to acute—, with numerous small, clavate to constricted-cylindric, granular *pilocystidia*. The type material is meagre, and apparently the lamellae have been partially devoured by insects. (Singer 1957: 230.)

R. arnoldae Murr., Torrey Bot. Club Bull. 67: 57. 1940. Since the type was not located, a specimen, No. F 19111, collected and determined by Murrill, was studied, with notes as follows: *Spores* (Fig. 33) 9-12 × 7-9 μ, warts 0.8-1.3 μ high, isolated or some catenulate, no fine lines. *Epicutis* (Fig. 296) composed of a turf of somewhat nodulose, subulate hyphae; no *pilocystidia*. (Singer Lilloa 22: 711, footnote, says *R. arnoldae* is a typical Florida race of the *Xerampelina*-group.)

R. atropurpurea Pk., New York State Mus. Ann. Rept. 41: 75. 1888. *Spores* (Fig. 98) 8-11 × 7-8 μ, warts 0.8-1.2 μ high, isolated or catenulate, with a few fine lines. *Epicutis* (Fig. 255) composed of numerous scattered tufts of hyphae, with more or less repent hyphae between the tufts, and with buried and projecting clavate *pilocystidia*. (Singer 1942: 78 says this is a synonym of *R. xerampelina* Fr.)

R. aurantialutea Kauff., Michigan Acad. Sci. Rept. 11. 81. 1909. *Spores* (Fig. 58) 8-10 × 6.5-8 μ, warts 0.6-1.2 μ high, isolated or short-catenulate, with some fine lines. *Epicutis* (Fig. 282) composed of more or less erect, narrow hyphae with acute, rounded, or subcapitate apices. *Pilocystidia* clavate, banded 40-60 × 3-6 μ. Singer 1957: 266.)

R. australirosea Murr., Lloydia 8: 264. 1945. *Spores* (Fig. 42) 8-10.5 × 6.5-8 μ, warts 0.6-1.2 μ high, a few isolated, with broad bands and fine lines forming an incomplete reticulum. *Epicutis* (Fig. 297) composed of hyphae which are cylindric, nodulose, or ventricose, the apices at times appendiculate; *pilocystidia* not found. (Singer 1957: 215 states that the terminal elements of some hyphae are dermatocystidioid.)

R. basifurcata Pk., New York State Mus. Ann. Rept. 38: 90. 1885. *Spores* (Fig. 31) 6.8-7.5 × 5-6 μ, warts 0.1-0.2 μ high, isolated or with a few short bands. *Pleurocystidia* 56-132 × 6-14 μ, fusoid to subclavate, at times appendiculate or subcapitate, banded; *cheilocystidia* 37-70 × 6-12 μ, clavate, fusoid or subulate. *Epicutis* (Fig. 318) composed of erect or ascendant hyphae which may be septate, often constricted-nodulose, the terminal element subulate or clavate. (No studies reported by Singer.)

R. beardslei Burl., Mycologia 31: 499. 1939. *Spores* (Fig. 3) 9-11 × 5-7 μ, warts 0.1 μ or less in height, with few to many fine lines forming a partial reticulum. *Epicutis* (Fig. 292) composed of narrow, gelatinous, erect hyphae cylindric or nodulose, apices rounded or acute, with an occasional *pilocystidium*. (Singer 1957: 253.)

R. blackfordae Pk., New York State Mus. Bull. 139: 43. 1910. *Spores* (Fig. 40) 8-10 × 7-8 μ, warts 0.4-0.6 μ, rarely 1.0 μ high, with some broad

bands and a few fine lines. *Epicutis* (Fig. 262) composed of a tangle of erect and ascendant hyphae, and clavate to elongate *pilocystidia*, all forming a turf. (Singer 1957: 250.)

R. borealis Kauff., Mich. Acad. Sci. Rept. 11: 69. 1909. *Spores* (Fig. 91) 8-10 × 7-9 μ, warts 0.8-1.5 μ, isolated or catenulate, a few short lines. *Pleurocystidia* 60-77 × 5-10 μ, versiform (ventricose, cylindric, clavate, obclavate), apices rounded or appendiculate, granular or empty; *cheilocystidia* 48-56 × 6-10 μ, ventricose, bottle-shaped, clavate, empty or granular, apices acute, mucronate, or subcapitate. *Epicutis* (Fig. 234) a turf of irregularly-shaped hyphae, apices acute, rounded, or subcapitate; no *pilocystidia*. (No studies reported by Singer.)

R. brevipes Pk., New York State Mus. Ann. Rept. 54: 178. 1901. *Spores* (Fig. 113) 9-11 × 8.5-10 μ, warts 1.0-1.7 μ high, with a continuous or broken reticulum of fine lines. *Epicutis* (Fig. 253) not differentiated; the cuticle is composed of repent hyphae. (Singer 1947: 173-174 states that *R. brevipes* Pk. is a synonym of *R. delica* Fr.)

R. brunneipes Murr., Lloydia 7: 310. 1944. *Spores* (Fig. 112) 8-10.5 × 7-9 μ, warts variable in height: many 0.2-0.5 μ, others 0.8-1.2 μ high, isolated or catenulate, with some fine lines. *Pleurocystidia* 43-76 × 6-9 μ, fusoid to subventricose, apices blunt or acute, empty; *cheilocystidia* 36-45 × 6-8 μ, clavate or subfusoid, apices acute or appendiculate, empty. *Epicutis* (Fig. 172) composed of slender, erect, more or less nodulose hyphae, a few branched; *pilocystidia* present. (No studies reported by Singer.)

R. brunneola Burl., North American Flora 9: 233. 1915. *Spores* (Fig. 30) 6.5-8 × 5.4-6.5 μ, warts 0.1-0.2 μ high, isolated or a few short-catenulate, a few short fine lines. *Epicutis* (Fig. 286) composed of a palisade of septate, constricted hyphae, the terminal cell more or less acute, with one to three or more basal cells; no *pilocystidia*. (Singer 1957: 176.)

R. burkei Burl., Mycologia 16: 21. 1924. *Spores* (Fig. 7) 8-9.5 × 6.5-7.5 μ, warts 0.1 μ or less in height, fine lines forming a rather complete reticulum. *Epicutis* (Fig. 270) composed of more or less nodulose hyphae, the apices rounded or acute, with numerous banded *pilocystidia*. (Singer 1942: 79.)

R. chlorinosma Burl., Mycologia 16: 22. 1924. The type was not studied. The following notes are based on my observations of Burke's specimen, No. 799, Montgomery, Alabama: *Spores* (Fig. 47) 7-8.5 × 5.5-6.5 μ, warts 0.1 μ high, isolated or with a few fine lines. *Epicutis* (Fig. 196) composed of a palisade of septate, constricted hyphae, the terminal elements subulate, the basal cells sphaerocyst-like, the epicuticular elements resting on a pseudoparenchymatous hypodermium. The epicutis is structurally of the *virescens*-type. (Singer 1957: 193.)

R. cinerascens Beardslee, Elisha Mitchell Sci. Soc. Jour. 33: 164. 1918. The following notes are based, not on the type, but on Beardslee's collection from Asheville, 1917, on deposit at the New York Botanical Garden: *Spores* (Fig. 105) 7-9 × 6.3-7.5 μ, warts 0.2-0.4 μ high, isolated, with some fine lines, at times catenulate. *Epicutis* (Fig. 265) composed of a turf of septate-constricted hyphae, apices rounded or subcapitate; with several clavate, banded *pilocystidia*. (Singer 1942: 78-79.)

R. compacta Frost & Pk., New York State Mus. Ann. Rept. 32: 32. 1879. The following notes are based on Peck's Sandlake collection which is mentioned first in his original description. *Spores* (Fig. 63) 7-9.5 × 6-8 μ, warts 0.1-0.4 μ high, fine lines forming a reticulum. *Epicutis* (Fig. 259) not differentiated; the cuticle is composed of repent, brownish hyphae. (Singer 1943: 143.)

R. corallina Burl., North American Flora 9: 213. 1915. *Spores* (Fig. 103) 7.5-9 × 5.7-6.5 μ, warts usually less than 0.1 μ high, rarely 0.2 μ high, fine lines forming an indistinct reticulum. *Pleurocystidia* 46-68 × 6-10 μ, fusoid to ventricose, occasionally appendiculate, empty or banded; *cheilocystidia* 32-48 × 5-7 μ, ventricose, at times appendiculate, some banded. *Epicutis* (Fig. 239) composed of irregularly constricted, somewhat septate, erect hyphae, apices more or less acute; no *pilocystidia*. (No studies reported by Singer.)

R. craetegorum Murr., Florida Acad. Sci. Jour. 8: 181. 1945. *Spores* (Fig. 90) 8.5-10 × 7-8.5 μ, warts 0.6-1.0 μ high, isolated or a few catenulate, with fine lines. *Pleurocystidia* 58-78 × 7-12 μ, clavate, ventricose, at times constricted, apices rounded or more often appendiculate, empty, granular, or banded; *cheilocystidia* 41-53 × 7-12 μ, ventricose, clavate, or subfusoid, apices rounded or mucronate, empty. *Epicutis* (Fig. 233) composed of a turf of hyphae which are somewhat septate and constricted, some hyphae with swollen cells; no *pilocystidia*. (No studies reported by Singer.)

R. cremea (Murr.) Singer, Lilloa 22: 711. 1949. *Spores* (Fig. 106) 8.5-11 × 5.4-6.3 μ, warts 0.1 μ or less in height, rarely 0.2 μ high, fine lines forming a reticulum. *Epicutis* (Fig. 285) composed of more or less nodulose hyphae, usually tapering at apex, erect or ascendant; no *pilocystidia*. (Singer 1957: 209 lists *R. heterospora* var. *cremea* Murr. as a synonym.)

R. cremeirosea Murr., Lloydia 8: 265. 1945. *Spores* (Fig. 137) 8-11 × 7.5-10 μ, warts 0.8-1.4 μ high, isolated or with a few indistinct fine lines. *Pleurocystidia* 50-76 × 3-10 μ, ventricose to cylindric-constricted, apices acute or appendiculate, empty, granular, or banded; *cheilocystidia* 42-48 × 7-9 μ, ventricose or obclavate, apices mucronate to rounded, empty. *Epicutis* (Fig. 237) composed of more or less erect, cylindric or constricted hyphae, the apices acute or rounded, rarely septate; no *pilocystidia*. (No studies reported by Singer.)

R. cremeirubra Murr., Lloydia 8: 265. 1945. *Spores* (Fig. 101) 8-9.5 × 7-8 μ, warts 0.4-0.6 μ high, a few isolated, catenulate, with an occasional fine line. *Pleurocystidia* 42-76 × 7-10 μ, ventricose to fusoid, often long-appendiculate, empty or granular; *cheilocystidia* 27-43 × 5-7 μ, ventricose, mucronate or appendiculate, empty or granular. *Epicutis* (Fig. 236) composed of scattered, narrow (1-3), erect or ascendant hyphae, some broader and septate; no *pilocystidia*. (No studies reported by Singer.)

R. crustosa Pk., New York State Mus. Ann. Rept. 39: 41. 1887. *Spores* (Fig. 29) 7-8 × 5.7-6.5 (7.5) μ, warts 0.2-0.3 μ high, at times shorter, isolated, or at times catenulate or with fine lines. *Epicutis* (Fig. 195) composed of a turf of versiform hyphae with tapering apices, which arise from a pseudoparenchymatous hypodermium,—a *virescens*-type of epicutis; no *pilocystidia*. (Singer 1957: 197.)

R. cystidiosa Murr., Torrey Bot. Club Bull. 67: 57. 1940. *Spores*

(Fig. 46) 9-12 × 9-10 μ, warts more or less cylindric, 0.8-1.8 μ high, a few isolated, some catenulate, with some fine lines. *Epicutis* (Fig. 281) composed of erect hyphae which are somewhat constricted; *pilocystidia* clavate, banded. (Singer 1957: 228.)

R. diaboli Singer, Lilloa 22: 719. 1949. *Spores* (Fig. 121) 8-10.5 × 7-8.5 μ, warts 0.5-0.7 μ high, isolated or catenulate, with some fine lines. *Epicutis* (Fig. 283) composed of erect hyphae, some slightly nodulose, apices attenuated, with numerous granular to banded *pilocystidia*. (Singer 1957: 270.)

R. earlei Pk., New York State Mus. Bull. 67: 24. 1903. *Spores* (Fig. 102) 5.5-7.5 × 4-5 μ, warts 0.2-0.3 μ high, isolated, rarely with a few short, inconspicuous, fine lines. *Epicutis* (Fig. 266) composed of erect, septate, constricted hyphae; *pilocystidia* none. (Singer 1957: 143.)

R. eccentrica Pk., New York State Mus. Bull. 150: 61. 1911. *Spores* (Fig. 104) 7-9 × 5.7-7.5 μ, warts very short punctations, often indistinct and then the wall appears smooth, with a few faint lines. *Epicutis* (Fig. 182) not differentiated; the cuticle composed of repent hyphae, with a few more or less erect free ends. (Singer 1957: 146 considers this to be a subspecies of *R. nigricans* Fr.)

R. emeticiformis Murr., Mycologia 30: 362. 1938. *Spores* (Fig. 75) 8-11 × 7-9 μ, warts 0.6-1.3 μ high, isolated or with few to many fine lines. *Epicutis* (Fig. 209) composed of slender, more or less nodulose to cylindric hyphae, with several clavate, minutely banded *pilocystidia*. (Singer 1957: 232 doubtfully calls this a synonym of *R. emetica* ssp. *lacustris* Singer, differing in its darker pileus.)

R. ferrotincta Singer, Mycologia 37: 428. 1945. Notes on co-type, No. F 1889c: *Spores* (Fig. 34) 7-9 × 6.3-7 μ, warts 0.3-0.6 μ high, isolated, some nearly catenulate, with some fine lines. *Epicutis* (Fig. 280) composed of erect, narrow, clavate to fusoid hyphae, the apices rounded to acute, with more or less buried *pilocystidia*. (Singer 1945: 429 does not mention *pilocystidia*.)

R. flaviceps Pk., New York State Mus. Ann. Rept. 53: 843. 1901. *Spores* (Fig. 153) 7.5-9.5 × 7-7.5 μ, warts blunt, 0.4-0.6 μ high, with some ridges and fine lines. *Epicutis* (Fig. 264) composed of erect hyphae, at times branched, with clavate, banded *pilocystidia*. (Singer 1957: 254.)

R. flocculosa Burl., North American Flora 9: 213. 1915. *Spores* (Fig. 52) 7-9 × 5.5-7 μ, warts 0.2-0.3 μ high, with a few fine lines. *Epicutis* (Fig. 288) composed of tufts of erect hyphae which are septate-constricted, the apices often tapering; no *pilocystidia*. (Singer 1942: 75.)

R. floridana Murr., Torrey Bot. Club Bull. 67: 145. 1940. *Spores* (Fig. 109) 8-11.5 × 6.3-8 μ, warts 0.5-0.8 μ high, isolated, rarely short-catenulate, a few indistinct fine lines. *Epicutis* (Fig. 189) composed of erect hyphae, at times in tufts, accompanied by clavate, banded *pilocystidia*. (Singer 1957: 218 regards this as a synonym of *R. xerampelina* var. *semirubra* Singer.)

R. foetentula Pk., New York State Mus. Bull. 116: 85. 1907. *Spores* (Fig. 67) 8-10 × 7-8 μ, warts 0.7-1.2 μ high, isolated, with ridges and fine lines. *Epicutis* (Fig. 181) composed of tufts of hyphae, at times con-

stricted; these tufts constitute the granules seen on the surface of the pileus; no *pilocystidia*. (Singer 1943: 114 reports on spore ornamentation but does not mention the epicutis.)

R. fosteriana Murr., Lloydia 6: 210. 1943. *Spores* (Fig. 134) 7-8.5 × 5-6.3 μ, warts 0.2-0.4 μ high, at times mere punctations, isolated or slightly catenulate, with a few short, indistinct fine lines. *Pleurocystidia* 50-66 × 7-12 μ, ventricose, appendiculate, empty or banded; *cheilocystidia* 48-63 × 6-8 μ, ventricose, more or less mucronate or appendiculate, granular or banded. *Epicutis* (Fig. 279) rarely as scattered, more or less erect hyphae; with banded *pilocystidia*, the apices rounded to appendiculate. (No studies reported by Singer.)

R. fragilioides Murr., Lloydia 8: 265. 1945. *Spores* (Fig. 100) 7-9 × 6.5-7.5 μ, warts 0.5-0.8 μ high, with some short bands, few to many fine lines. *Epicutis* (Fig. 173) composed of more or less erect, somewhat tangled hyphae, the apices acute to tapering; with clavate, banded or granular *pilocystidia*. (Singer 1957: 234 places this species in synonomy with *R. emetica* ssp. *emeticella* (Singer) Singer.)

R. furcatifolia Murr., Lloydia 6: 210. 1943. *Spores* (Fig. 84) 8-10 × 7-8.5 μ, warts 0.8-1.3 μ high, isolated, with many fine lines some not reaching another wart, at times short-catenulate. *Epicutis* (Fig. 214) composed of cylindric to nodulose-constricted hyphae, the apices acute to subcapitate; *pilocystidia* numerous, banded, the apices acute to subcapitate. (Singer 1957: 151 places this species in synonomy with *R. subsericeonitens* Murr.)

R. glauca Burl., North American Flora 9: 222. 1915. The following notes are based on a study of Burlingham's collection No. 18-1911: *Spores* (Fig. 51) 7-8.5 × 5-5.7 μ, warts 0.1-0.3 μ high, isolated, with a few fine lines. *Pleurocystidia* 50-63 × 7-10 μ, ventricose, more or less appendiculate, at times subcapitate, granular or banded; *cheilocystidia* 33-54 × 5-7 μ, ventricose, apices acute or capitate, empty or banded. *Epicutis* (Fig. 240) composed of erect hyphae, scattered or in tufts, some septate and slightly constricted, others non-septate, the apices tapering; no *pilocystidia*. (No studies reported by Singer.)

R. glaucescentipes Murr., Lloydia 6: 211. 1943. *Spores* (Fig. 83) 7-8.5 × 6.3-7.5 μ, warts 0.7-1.0 μ high, some isolated, some with fine lines which may not always reach another wart, a few catenulate. *Epicutis* (Fig. 202) composed of a few erect or ascendant hyphae with acute apices; no *pilocystidia*. (Singer 1957: 202 reports "strange elongate elements" in the epicutis.)

R. granulata Pk., New York State Mus. Ann. Rept. 53: 843. 1901. *Spores* (Fig. 35) 7-8.5 × 5.5-6.5 μ, warts 0.4-0.8 μ high, most 0.5 μ or less, isolated or with a few short lines. *Epicutis* (Fig. 245) composed of tufts (squamules) of pale brownish, septate hyphae which may be constricted and the apices acute or capitate. In areas between tufts, the surface hyphae are repent. No *pilocystidia* found. (Singer 1957: 160 reports *pseudocystidia* on the pileus.)

R. granulosula Murr., Lloydia 6: 211. 1943. *Spores* (Fig. 48) 7.5-9 × 7-8 μ, warts 0.5-1.2 μ high, with a reticulum of broad bands and a few fine lines. *Pleurocystidia* 66-86 × 10-15 μ, ventricose, apices tapering,

empty; *cheilocystidia* 51-66 × 6-10 μ, ventricose, cylindric, or constricted, apices acute, at times appendiculate, empty. *Epicutis* (Fig. 257) composed of tufts of hyphae which may be brown, may arise from one or two basal cells, the apices more or less subnlate; no *pilocystidia*. (No studies reported by Singer.)

R. heterospora Beardslee, Mycologia 26: 259. 1934. The following notes are based on a study of a collection by Beardslee labelled "type woods," November 16, 1938: *Spores* (Fig. 1) 8-13.5 × 4.5-6.3 μ, warts less than 0.1 μ high or nearly smooth, isolated or with an indistinct reticulum of fine lines. *Epicutis* (Fig. 183) scarcely differentiated; the cuticle composed of repent hyphae with an occasional more or less erect hypha; no *pilocystidia*. (Singer 1957: 173.)

R. heterosporoides Murr., Lloydia 7: 310. 1944. *Spores* (Fig. 25) 7-8 × 4-5 μ, warts less than 0.1 μ high or nearly smooth, isolated or with a few fine lines. *Epicutis* (Fig. 175) composed of a palisade of cells with rounded or acute apices, all arising from a pseudoparenchymatous hypodermium,—a *virescens*-type of epicutis. (Singer 1957: 196.)

R. hixsoni Murr., Lloydia 6: 212. 1943. *Spores* (Fig. 41) (8.5) 11-13.5 × 7.5-10.5 μ, warts nearly cylindric, 1.2-1.7 μ high, isolated, rarely catenulate, with a few fine lines which may not reach the next wart. *Epicutis* (Fig. 199) composed of hyphae, scattered or in tufts, more or less clavate, the apices acute to subcapitate; no *pilocystidia*. (Singer 1957: 209.)

R. incarnaticeps Murr., Torrey Bot. Club Bull. 67: 277. 1940. *Spores* (Fig. 64) 7.5-11 × 6.3-8.5 μ, warts 0.8-1.3 μ, more or less cylindric, some isolated, others with fine lines and coarse bands forming an incomplete reticulum. *Epicutis* (Fig. 278) composed of more or less erect, narrow hyphae, the apices rounded or acute; *pilocystidia* with species acute or clavate. (Singer 1957: 219.)

R. inedulis Murr., Lloydia 7: 311. 1944. *Spores* (Fig. 28) 8-10.5 × 7-9 μ, warts 0.2-0.5 μ high, some isolated, others with broad ridges and a few fine lines. *Pleurocystidia* 56-88 × 9-12 μ, ventricose to subfusoid, appendiculate, the appendages acute to capitate, banded; *cheilocystidia* 45-58 × 7-10 μ, ventricose, apices rounded to appendiculate, empty. *Epicutis* (Fig. 276) composed of hyphae, clavate or constricted, the apices acute; *pilocystidia* clavate, or with apices appendiculate, granular to minutely banded. (No studies reported by Singer.)

R. leucomodesta Singer, Sydovia 11: 178. 1957. *Spores* (Fig. 12) 7-9 × 5.7-7 μ, warts 0.5-0.7 (1.0) μ high, mostly isolated, a few catenulate. *Epicutis* (Fig. 275) composed of hyphae which are scattered to clustered, septate, the apices acute to rounded; *pilocystidia* numerous, banded or granular, somewhat cylindric, apices acute to rounded.

R. levispora Murr., Lloydia 6: 212. 1943. The following notes are based on a study of Murrill's No. F 17449: *Spores* (Fig. 156) 7.5-9.5 × 6.3-8 μ, warts 0.1-0.2 μ high or less, with fine lines and a few short ridges forming a reticulum. *Epicutis* (Fig. 176) composed of a turf of constricted-nodulose hyphae with rounded sub-acute apices; no *pilocystidia*. (Singer 1957: 191 regards this species as a synonym of *R. ochroleucoides* Kauff.)

R. levyana Murr., Lloydia 7: 311. 1944. *Spores* (Fig. 152) 9-12 × 8-10 μ, warts 0.5-1.3 μ high, isolated or with some fine lines, at times short-catenulate. *Epicutis* (Fig. 301) composed of cylindric and non-septate or constricted and septate hyphae, with a few rather inconspicuous, granular to minutely banded *pilocystidia*. (Singer 1957: 218 regards this as a synonym of *R. xerampelina* var. *semirubra* Sing.)

R. lividirosea Murr., Torrey Bot. Club Bull. 67: 278. 1940. *Spores* (Fig. 127) 7.5-10 × (5.5) 7-8 μ, warts 0.6-0.8 μ high, isolated or with bands and fine lines forming somewhat of a reticulum. *Epicutis* (Fig. 258) composed of scattered tufts, the hyphae more or less subulate, arising from one or two basal cells; no *pilocystidia*. (Singer 1957: 229.)

R. luteispora Murr., Lloydia 7: 311. 1944. *Spores* (Fig. 44) 7-8.5 × 5-6.3 μ, warts 0.2-0.5 μ high, a few isolated, bands and lines forming a more or less complete reticulum. *Pleurocystidia* 33-48 × 6-8 μ, ventricose, appendiculate, mostly buried, scattered, inconspicuous, more numerous near the edges of the lamellae, granular; *cheilocystidia* 30-45 × 4-6 μ, ventricose to cylindric, faintly constricted, apices acute or mucronate, empty. *Epicutis* (Fig. 277) composed of scattered to dense erect hyphae, some slender and non-septate, others broader, septate-constricted, the terminal element somewhat granular; no *pilocystidia*. (No studies reported by Singer.)

R. luteobasis Pk., Torrey Bot. Club. Bull. 31: 179. 1904. *Spores* (Fig. 66) 7-9 × 6-7 μ, warts 0.6-0.9 μ high, ridges and fine lines forming a reticulum. *Epicutis* (Fig. 315) composed of a turf of hyphae which may occur in tufts, some slender-cylindric, others broader and septate, clavate, spathulate, or subfusoid; no *pilocystidia*. (Singer 1957: 206.)

R. lutescentifolia Murr., Lloydia 8: 267. 1945. *Spores* (Fig. 62) 7.5-9 × 6-7 (8) μ, warts 0.2-0.3 μ high, broad bands and fine lines forming a reticulum. *Epicutis* (Fig. 174) composed of a turf of hyphae which are clavate to fusoid, often appendiculate, occasionally septate; no *pilocystidia*. (Singer 1957: 191 regards this as a synonym of *R. ochroleucoides* Kauff.)

R. macropoda Singer, Bull. Soc. Mycol. Fr. 55: 277. 1939. The following notes are based on a specimen collected and determined by Singer, V-270, Mountain Lake, Virginia: *Spores* (Fig. 145) 7.5-10 × 7-8.5 μ, warts 0.6-1.2 μ high, isolated, some catenulate, with a few fine lines. *Epicutis* (Fig. 210) composed of a turf of hyphae imbedded in a transparent gelatinous zone and disposed at more or less at 45°-angle, with clavate, banded *pilocystidia*. (Singer 1957: 268.)

R. maculosa Murr., Lloydia 6: 212. 1943. The following notes are based on a study of a Florida specimen collected and determined by Murrill: *Spores* (Fig. 132) 7-8.5 × 5-6 μ, warts 0.1 μ high, isolated or with a few fine connecting lines. *Epicutis* (Fig. 294) composed of hyphae which are septate-constricted, the cells progressively larger downward, and arising from a zone of pseudoparenchyma,—a *virescens*-type of epicutis; no *pilocystidia*. (Singer 1957: 193-194 regards this as a synonym of *R. chlorinosma* Burl.)

R. magna Beards., Elisha Mitchell Sci. Soc. Jour. 33: 183. 1918. The following notes are based on a specimen collected and determined by Beardslee, Asheville, North Carolina, August 10, 1917: *Spores* (Fig. 22) 8.5-11 × 7.5-10 μ, warts 0.2-0.4 μ high, with a reticulum of broad bands

and fine lines. *Epicutis* (Fig. 224) composed of hyphae which are clavate, cylindric, or fusoid, hyaline or brownish, with rounded or tapering apices; with clavate, banded *pilocystidia*. (Singer 1942: 80.)

R. magnifica Pk., New York State Mus. Bull. 67: 24. 1903. *Spores* (Fig. 54) 7-9 × 5.7-7 μ, warts 0.1-0.4 μ, isolated or with a few fine lines which fail to reach another wart. *Epicutis* (Fig. 249) in young pilei composed of cylindric to clavate hyphae, apices acute, rounded, or capitate; in mature pilei, the epicuticular hyphae slough away leaving a cuticular surface of repent hyphae. *Pilocystidia* none. (Singer 1943: 142 assumes this to be a synonym of *R. polyphylla* Pk.)

R. mariae Pk., New York State Mus. Ann. Rept. 24: 74. 1872. *Spores* (Fig. 65) 7.5-9.5 × 6.5-8 μ, warts 0.6-1.0 μ high. *Epicutis* (Fig. 197) composed of a turf of septate-constricted hyphae, with one or more basal cells, apices tapering or filiform; no *pilocystidia*. (Singer 1957: 185.)

R. modesta Pk., New York State Mus. Bull. 116: 78. 1907. *Spores* (Fig. 140) 6.3-9 × 5-6.5 μ, warts 0.1-0.4 μ high, isolated, at times catenulate or with fine lines. *Epicutis* (Fig. 289) composed of a turf of hyphae in a gelatinous zone, the terminal elements subulate, often the hypha arises from a cell or a chain of 2-4 cells; clavate *pilocystidia* present. (Singer 1957: 179.)

R. mutabilis Murr., Torrey Bot. Club Bull. 67: 146. 1940. *Spores* (Fig. 60) 8-10.5 × 7.5-9 μ, warts 0.9-1.4 μ high, coarse and blunt, isolated, with some fine lines and a few short bands. *Epicutis* (Fig. 194) composed of more or less repent hyphae; scattered over the surface are pulverulent areas composed of brownish, slender, erect hyphae; no *pilocystidia*. (Singer 1957: 160.)

R. mutantipes Murr., Lloydia 8: 267. 1945. *Spores* (Fig. 86) 8-10 × 6.3-8 μ, warts 0.8-1.2 μ high, isolated with some short ridges and indistinct fine lines. *Pleurocystidia* 45-76 × 7-9 μ, ventricose, apices obtuse, acute, or mucronate, granular; *cheilocystidia* 35-54 × 5-8 μ, ventricose, apices acute or mucronate-subcapitate, granular or banded. *Epicutis* (Fig. 242) composed of tufts of hyphae which are usually either cellular or arise from a basal cell; no *pilocystidia*. (No studies reported by Singer.)

R. nigrescentipes Pk., Torrey Bot. Club Bull. 33: 214. 1906. *Spores* (Fig. 70) 7-9 × 5.7-7.5 μ, warts 0.4-0.6 μ high, isolated or with bands and fine lines forming an incomplete reticulum. *Epicutis* (Fig. 256) composed of a turf of hair-like hyphae which seem gelatinous, each hypha arising from rounded basal cell, all resting on a zone of tangentially parallel hyphae; no *pilocystidia*. (Singer 1943: 148.)

R. nigrodisca Pk., Fur Seals North Pacific 3: 583. 1899. *Spores* (Fig. 130) 8.5-10 × 7-7.5 μ, warts 0.2-0.4 μ high, ridges and fine lines forming a more or less complete reticulum. *Epicutis* (Fig. 228) composed of erect hyphae which are somewhat constricted, with clavate *pilocystidia*. (Singer 1943: 149 says this does not seem to be different from *R. emetica* ssp. *alpestris* (Bond.) Singer,—an alpine form.)

R. novispora Murr., Mycologia 36: 309. 1944. *Spores* (Fig. 53) 8-10 × 4.5-6 μ, warts 0.1 μ or less in height, isolated or some short-catenulate, and with some fine lines. *Pleurocystidia* 50-91 × 7-13 μ, ventricose, fusoid, or irregular, apices acute, at times appendiculate, granular; *cheilocystidia*

33-45 × 5-7 μ, ventricose, apices blunt, acute, or at times appendiculate, empty, granular, or banded. *Epicutis* (Fig. 304) composed of erect hyphae which are cylindric, clavate, or fusoid, at times constricted; *pilocystidia* numerous, clavate or subcapitate. (No studies reported by Singer.)

R. obscuriformis Murr., Lloydia 7: 312. 1944. *Spores* (Fig. 150) 8-9.5 × 6.3-8 μ, warts 0.5-0.8 μ high, broad bands and fine lines forming an incomplete reticulum. *Pleurocystidia* 36-64 × 5-10 μ, ventricose, often constricted, appendiculate, empty; *cheilocystidia* 30-43 × 6-11 μ, ventricose, appendiculate, empty. *Epicutis* (Fig. 260) composed of erect to ascendant hyphae, with rather rare and inconspicuous *pilocystidia*. (No studies reported by Singer.)

R. ochroleuciformis Murr., Lloydia 8: 267. 1945. *Spores* (Fig. 21) 7-8 × 5.5-7 μ, warts 0.1-0.2 μ high, rather strongly banded and with a few fine lines. *Pleurocystidia* 52-67 × 5-10 μ, ventricose, appendiculate, granular or banded; *cheilocystidia* 35-52 × 4-8 μ, ventricose, bottle-shaped, or subclavate, apices appendiculate or mucronate, empty or banded. *Epicutis* (Fig. 190) composed of erect, somewhat scattered hyphae; no *pilocystidia*. (No studies reported by Singer.)

R. ochroleucoides Kauff., Mycologia 9: 165. 1917. *Spores* (Fig. 9) 8.5-10 × 7-8 μ, warts 0.1-0.2 (0.3) μ high, bands and fine lines forming a reticulum. *Epicutis* (Fig. 188) composed of a turf of more or less erect hyphae; no *pilocystidia*. (Singer 1957: 191.)

R. ochrophylla Pk., New York State Mus. Ann. Rept. 50: 100. 1897. *Spores* (Fig. 147) 8.5-12 × 7-9 μ, warts 0.5-0.8 μ high, at times isolated, again catenulate, with a few short lines. *Epicutis* (Fig. 238) composed of erect hyphae, at times slightly constricted, apices rounded or slightly tapering; no *pilocystidia*. (Singer 1939: 252 says that this is a synonym of *R. olivacea* (Schaeff. ex Schw.) Fr.)

R. palustris Pk., New York State Mus. Ann. Rept. 53: 842. 1900. *Spores* (Fig. 80) 8-10 × 5.5-8 μ, warts 0.3-0.8 μ high, at times isolated, often short-catenulate and with a few fine lines. *Epicutis* (Fig. 232) composed of erect hyphae which are slender with tapering or acute apices; *pilocystidia* clavate, numerous. (Singer 1957: 242 lists this in synonymy with *R. putchella* Borszcz.)

R. partirosea Murr., Lloydia 8: 268. 1945. The following notes are based on a study of a topotype collection by Murrill: *Spores* (Fig. 94) 7.8-9.3 × 7-8 μ, warts 0.2 μ high or less, at times catenulate, with a few fine lines. *Pleurocystidia* 50-71 × 7-11 μ, clavate, apices rounded or mucronate, at times appendiculate, banded; *cheilocystidia* 28-50 × 5-10 μ, clavate, capitate or mucronate, empty or banded. *Epicutis* (Fig. 177) composed of erect, slender hyphae, with clavate, more or less banded *pilocystidia*. (No studies reported by Singer.)

R. patriotica Murr., Mycologia 40: 635. 1948. *Spores* (Fig. 78) 8-11 × 7-9 μ, warts 0.3-0.5 μ high, isolated or catenulate, with a few fine lines. *Pleurocystidia* 47-68 × 6-12 μ, clavate, often appendiculate, granular; *cheilocystidia* 34-52 × 6-10 μ, clavate, fusoid or ventricose, acute, appendiculate, or capitate. *Epicutis* (Fig. 293) composed of numerous pyramidal tufts of hyphae, at times tinged brownish; *pilocystidia* banded or granular, clavate. (No studies reported by Singer.)

R. peckii Singer, Mycologia 35: 147. 1943. The following notes are based on a study of a collection determined by Singer: *Spores* (Fig. 129) 8-9.5 × 7-8 μ, warts 0.4-0.6 μ high, fine lines forming a more or less complete reticulum. *Epicutis* (Fig. 207) composed of erect or ascendant hyphae, with clavate *pilocystidia*-like bodies. (Singer 1943: 147 proposed this binomial for *R. purpurina* Schulzer, *sensu* Peck. He (1957: 217) regards the pilocystidia-like bodies as bluing hyphal ends.)

R. pectinatoides Pk., New York State Mus. Bull. 116: 43. 1907. *Spores* (Fig. 61) (6.5) 7.5-9 × 5.5-7.5 μ, warts 0.4-0.6 μ high, a few isolated, mostly short-catenulate with fine lines forming an incomplete reticulum. *Epicutis* (Fig. 250) composed of loosely arranged, erect or ascendant hyphae, with a few conducting hyphae. (Singer 1957: 164.)

R. perlactea Murr., Lloydia 6: 213. 1943. *Spores* (Fig. 146) 10-13.5 × 8.5-10.5 μ, warts 0.8-1.7 μ high, somewhat cylindric, some isolated, with fine lines. *Epicutis* (Fig. 272) composed of clavate, fusoid, or cylindric hyphae, the apices acute or subcapitate; *pilocystidia* clavate, numerous. (Singer 1957: 232 regards this as a synonym of *R. emetica* ssp. *lacustris* Singer,—merely a white form.)

R. perplexa Burl., Mycologia 10: 96. 1918. *Spores* (Fig. 16) 9-11.8 × 7-8.5 μ, warts 0.8-1.5 μ high, isolated or with some fine lines forming an incomplete reticulum. *Epicutis* (Fig. 268) composed of gelatinized, loosely arranged hyphae, with several cylindric to clavate *pilocystidia*. (Singer 1957: 216.)

R. pervirginea Murr., Lloydia 8: 268. 1945. *Spores* (Fig. 128) 8-10 × 7-8.5 μ, warts 0.5-1.0 μ high, rarely catenulate, fine lines forming a more or less complete reticulum. *Epicutis* (Fig. 291) composed of versiform hyphae (cylindric, nodulose, ampullaceous, the apices rounded or acute); *pilocystidia* somewhat fusoid to irregular, granular to banded. (Singer 1957: 232 doubtfully lists this as a synonym of *R. emetica* ssp. *lacustris* Singer, pointing out that in *R. pervirginea* the spores are slightly smaller.)

R. pinetorum Murr., Torrey Bot. Club Bull. 66: 155. 1939. *Spores* (Fig. 81) 8.5-10 × 7-8 μ, warts 0.8-1.4 μ high, some isolated, with some fine lines. *Pleurocystidia* 47-61 × 7-8 μ, ventricose, acute or appendiculate, granular or banded; *cheilocystidia* 41-45 × 3-5 μ, fusoid, acute or appendiculate, empty. *Epicutis* (Fig. 307) composed of erect or ascendant hyphae which are cylindric, constricted, apices more or less tapering; *pilocystidia* numerous. (No studies reported by Singer.)

R. pinicola Murr., Lloydia 6: 213. 1943. *Spores* (Fig. 82) 9-10.5 × 7-8.5 μ, warts 0.6-1.0 μ high, more or less cylindric, isolated or with some fine lines. *Pleurocystidia* 54-64 × 5-11 μ, ventricose, at times constricted, apices appendiculate, empty or granular; *cheilocystidia* 47-55 × 7-8 μ, ventricose, clavate, or obclavate, mucronate or appendiculate, granular or banded. *Epicutis* (Fig. 267) composed of erect or ascendant hyphae which are cylindric, constricted, apices more or less tapering; *pilocystidia* numerous. (No studies reported by Singer.)

R. pinophila Murr., Florida Acad. Sci. Jour. 8: 182. 1945. *Spores* (Fig. 120) 8-11 × 7-9 μ, warts 0.8-1.2 μ high, isolated to catenulate, or with a few fine lines. *Epicutis* (Fig. 311) composed of septate or non-

septate hyphae, with scattered clavate *pilocystidia*. (Singer 1957: 221 places this in synonymy with *R. pusilla* Pk.)

R. praeclavipes Murr., Lloydia 6: 213. 1943. The following notes are based on a specimen collected and determined by Murrill, Gainesville, Florida, September 21, 1938: *Spores* (Fig. 142) 8-9 × 7-8 μ, warts 0.6-1.2 μ high, isolated, a few catenulate, some fine lines. *Pleurocystidia* few, 48-62 × 6-11 μ, fusoid or clavate, blunt, acute, or appendiculate, granular or banded; *cheilocystidia* few, 37-45 × 5-7 μ, fusoid or clavate, mucronate or appendiculate, empty or banded. *Epicutis* (Fig. 160) composed of more or less erect, cylindric to constricted hyphae, with clavate, granular to minutely banded *pilocystidia*. (No studies reported by Singer.)

R. praecompacta Murr., Lloydia 7: 312. 1944. *Spores* (Fig. 143) 7.5-9 × 6.3-7.5 μ, warts 0.5-0.7 μ high, isolated or with a few indistinct fine lines. *Pleurocystidia* 48-66 × 7-10 μ, ventricose or clavate, rounded or appendiculate, empty, granular, or banded; *cheilocystidia* 44-55 × 5-7 μ, clavate, fusoid, or constricted, apices acute or appendiculate, granular or minutely banded. *Epicutis* (Fig. 273) composed of numerous small tufts, between the tufts the hyphae are erect or ascendant; *pilocystidia* numerous. (No studies reported by Singer.)

R. praerubra Murr., Lloydia 6: 214. 1943. *Spores* (Fig. 119) 9-11 × 7.5-9 μ, warts 0.8-1.3 μ high, numerous, some isolated, with indistinct fine lines. Pleurocystidia 50-68 × 7-11 μ, ventricose, more or less constricted, acute or appendiculate, upper portion empty or banded; *cheilocystidia* 38-76 × 5-8 μ, fusoid to cylindric, often somewhat constricted, acute, appendiculate, or capitate. *Epicutis* (Fig. 206) composed of a turf of versiform hyphae—clavate, subcylindric, constricted, fusoid—non-septate; no *pilocystidia*. (No studies reported by Singer.)

R. praerubriceps Murr., Lloydia 6: 215. 1943. The following notes are based on a study of a specimen collected and determined by Murrill, F 19399: *Spores* (Fig. 141) 9-11 × 7-10 μ, warts 0.7-1.4 μ high, some isolated, with some fine lines. *Epicutis* (Fig. 161) composed of numerous tufts of slender hyphae; with many clavate, granular *pilocystidia*. (Singer 1957: 218 lists this as a synonym of *R. xerampelina* var. *semirubra* Singer.)

R. praetenuis Murr., Lloydia 6: 215. 1943. *Spores* (Fig. 135) 7-9 × 5.5-7 μ, warts 0.2-0.7 μ high, isolated, often with fine lines or bands, a few catenulate. *Epicutis* (Fig. 244) composed of hyphae which are erect or ascendant, more or less constricted, scattered or in loose tufts, some of the hyphae arising from a swollen basal cell, or more rarely a chain of two or more cells; no *pilocystidia* (Singer 1957: 204.)

R. pseudofoetens Murr., Lloydia 7: 312. 1944. *Spores* (Fig. 55) 7.5-9 × 6-7.5 μ, warts 0.3-0.5 μ high, with a few fine lines. *Pleurocystidia* few, 42-74 × 6-10 μ, fusoid, ventricose, or subcylindric, mucronate or appendiculate, banded; *cheilocystidia* 38-56 × 5-7 μ, fusoid or clavate, empty or banded. *Epicutis* (Fig. 162) composed of slender hyphae which are cylindric, often constricted; with clavate, granular *pilocystidia*. (No studies reported by Singer.)

R. pseudolepida Singer, Bull. Soc. Myc. Fr. 55: 251. 1939. The following notes are based on a study of a specimen, No. F 3418, collected and determined by Singer, Alachua County, Florida, July 30, 1947: *Spores*

(Fig. 72) 7-9.5 × 6.3-8 μ, warts 0.5-1.0 μ high, isolated or with some fine lines. *Epicutis* (Fig. 309) composed of a turf of slender hyphae, the terminal elements rounded, acute, or capitate; no *pilocystidia*. (Singer 1948: 114.)

R. pulchra Burl., Mycologia 10: 95. 1918. *Spores* (Fig. 85) 8-11 × 7-8.5 μ, warts 1.0-1.4 μ high, some short-catenulate, others isolated, with a few indistinct fine lines. *Epicutis* (Fig. 248) composed of loosely interwoven hyphae some of which are erect or ascendant, at times constricted; no *pilocystidia*. (Singer 1957: 213.)

R. pungens Beardslee, Elisha Mitchell Sci. Soc. Jour. 33: 196. 1918. The following notes are based on a specimen from Asheville, North Carolina, 1917, collected and named by Beardslee: *Spores* (Fig. 118) 9.5-12 × 7.5-10 μ, warts numerous, 0.7-1.3 μ high, isolated or occasionally short-catenulate, fine lines present or absent. *Pleurocystidia* 58-110 × 6-11 μ, fusoid to subclavate, often mucronate or appendiculate, banded; *cheilocystidia* 50-80 × 6-8 μ, fusoid or clavate, or irregular, rounded, at times mucronate, banded. *Epicutis* (Fig. 223) composed of a turf of slender, cylindric hyphae, and clavate, banded *pilocystidia*. (No studies reported by Singer.)

R. pusilla Pk., New York State Mus. Ann. Rept. 50: 99. 1897. *Spores* (Fig. 125) 7.5-9.5 × 5-7 μ, warts 0.4-0.6 μ high, some catenulate, others isolated, often with fine lines. *Epicutis* (Fig. 225) composed of a turf of more or less erect, at times constricted hyphae with rounded to acute apices; *pilocystidia* with banded contents. (Singer 1957: 221.)

R. pusilliformis Murr., Florida Acad. Sci. Jour. 8: 182. 1945. *Spores* (Fig. 123) 8-9.5 × 7-8 μ, warts 0.5-1.2 μ high, isolated or catenulate, with some fine lines. *Pleurocystidia* 50-63 × 6-12 μ, ventricose, acute or appendiculate, banded, granular, or empty; *cheilocystidia* 45-52 × 6-7 μ, ventricose, at times constricted, rounded, capitate, or acute, empty or banded. *Epicutis* (Fig. 254) composed of scattered to gregarious, erect or ascendant hyphae which are septate-constricted, the terminal element often appendiculate or subulate; with several *pilocystidia*. (No studies reported by Singer.)

R. regalis Murr., Torrey Bot. Club Bull. 67: 231. 1940. *Spores* (Fig. 87) 8.5-11 × 7.5-9 μ, warts 0.6-1.0 μ high, isolated or with some fine lines. *Pleurocystidia* 52-76 × 3-10 μ, ventricose to cylindric, acute or appendiculate, empty, granular, or banded; *cheilocystidia* 52-63 × 6-7 μ, ventricose or clavate, at times constricted, granular or banded. *Epicutis* (Fig. 306) composed of erect or ascendant hyphae which are usually constricted, the terminal element subulate to flask-shaped; no *pilocystidia*. (No studies reported by Singer.)

R. rimosa Murr., Lloydia 8: 270. 1945. *Spores* (Fig. 131) 6-8 × 5-6 μ, warts 0.1 μ or less in height, isolated or with a few fine lines. *Pleurocystidia* 48-85 × 6-10 μ, fusoid to subclavate, rounded or appendiculate, granular or banded; *cheilocystidia* 43-50 × 6-7 μ, clavate, at times constricted, rounded or appendiculate, granular or empty. *Epicutis* (Fig. 243) composed of a turf of hyphae which are more or less constricted to irregular, subulate or flask-shaped, each with a basal cell, the turf resting on a bed of pseudoparenchyma,—a *virescens*-type of epicutis. *R. rimosa*

Murr. agrees with *R rosei-isabellina* Murr. in essential respects, and therefore the former is reduced to synonymy. (No studies reported by Singer.)

R. rosei-isabellina Murr., Lloydia 6: 216. 1943. *Spores* (Fig. 74) 6-8 × 5-6 μ, warts less than 0.1 μ high, at times the wall appearing nearly smooth, isolated, with a few indistinct fine lines. *Pleurocystidia* 45-76 × 4-10 μ, ventricose, at times constricted, rounded or appendiculate, granular or banded; *cheilocystidia* 41-48 × 5-7 μ, clavate to ventricose, rounded or appendiculate, granular or empty. *Epicutis* (Fig. 308) composed of a turf of erect, more or less subulate hyphae, each with a basal cell, the turf resting on a bed of pseudoparenchyma,—a *virescens*-type of epicutis. (No studies reported by Singer.)

R. roseitincta Murr., Torrey Bot. Club Bull. 67: 278. 1940. *Spores* (Fig. 144) 8-10 × 7-8 μ, warts 0.6-1.0 μ high, isolated or with some indistinct fine lines. *Epicutis* (Fig. 241) composed of ascendant or erect hyphae which are variable: constricted, non-septate or septate, the apices rounded or acute; no *pilocystidia*. (Singer 1957: 211.)

R. rubrifolia Murr., Torrey Bot. Club Bull. 67: 232. 1940. *Spores* (Fig. 10) 8-10 × 7-8.5 μ, warts 0.4-0.8 (1.2) μ high, at times catenulate, broad bands and fine lines forming an incomplete reticulum. *Pleurocystidia* 60-88 × 6-11 μ, ventricose or clavate, at times irregular and slightly constricted, acute or appendiculate, empty or banded; *cheilocystidia* 48-54 × 2-7 μ, versiform (a filiform type numerous, some fusoid, others bottle-shaped), acute or appendiculate, empty, granular, or banded. *Epicutis* (Fig. 217) composed of erect or ascendant hyphae which are cylindric, subulate, capitate, or constricted; with clavate *pilocystidia*, and an occasional *oleiferous* hypha. (No studies reported by Singer.)

R. rubripurpurea Murr., Lloydia 6: 216. 1943. *Spores* (Fig. 50) 6.3-8 × 5-7.5 μ, warts usually 0.1 μ or less in height, at times 0.2-0.4 μ high, fine lines forming an incomplete reticulum. *Pleurocystidia* 50-62 × 5-10 μ, ventricose, acute or short-appendiculate, banded; *cheilocystidia* 40-50 × 5-6 μ, ventricose, clavate, or subcylindric, apices rounded or subcapitate, granular or banded. *Epicutis* (Fig. 204) composed of erect hyphae which are clavate, fusoid, at times constricted; no *pilocystidia*. (No studies reported by Singer.)

R. rugulosa Pk., New York State Mus. Ann. Rept. 54: 179. 1901. *Spores* (Fig. 56) 7-9 × 6-7 μ, warts 0.4-0.6 μ high, at times 0.1 μ or less, a few catenulate, with some fine lines. *Pleurocystidia* 46-66 × 6-8 (12) μ, clavate, ventricose, rounded or capitate, at times appendiculate, banded; *cheilocystidia* 38-45 × 5-7 μ, clavate, appendiculate, empty. *Epicutis* (Fig. 229) composed of a turf of hyphae which are cylindric, subclavate or subulate, at times nodulose; *pilocystidia* clavate, granular. (No studies reported by Singer.)

R. sericella Murr., Lloydia 7: 313. 1944. *Spores* (Fig. 77) 8-10 × 7-8 μ, warts 0.2-0.4 μ high, a few short-catenulate, many isolated, with some fine lines. *Pleurocystidia* 48-55 × 6-8 μ, inconspicuous, ventricose or fusoid, acute or appendiculate, granular or empty; *cheilocystidia* 33-48 × 5-6 μ, versiform (clavate, cylindric-capitate, at times constricted) empty or granular. (No studies reported by Singer.)

R. sericeonitens Kauff., Mich. Acad. Sci. Rept. 11: 84. 1909. *Spores* (Fig. 79) 8-9 × 6.3-7.5 μ, warts 0.9-1.2 μ high, isolated, rarely with one or two fine lines. *Epicutis* (Fig. 221) composed of a turf of erect to ascendant hyphae, which are cylindric to fusoid, the apices subulate or subcapitate; *pilocystidia* granular, more hyphoid in shape than cystidioid. (Singer 1957: 216.)

R. serissima Pk., New York State Mus. Bull. 139: 44. 1910. *Spores* (Fig. 92) 9-12 × (6.5) 8-10 μ, warts 0.6-1.2 μ high, numerous, mostly isolated, a few may be catenulate, and at times with a few indistinct fine lines. *Epicutis* (Fig. 212) composed of erect hyphae which tend to form tufts, the hyphae often irregularly nodulose, the apices rounded or acute; *pilocystidia* widely scattered, clavate. (Singer 1947: 78.)

R. simillima Pk., New York State Mus. Ann. Rept. 24: 275. 1872. *Spores* (Fig. 111) 7.5-9 × 6.3-7.5 μ, warts 0.1-0.2 μ high, or at times 0.5-0.7 μ high, fine lines forming a reticulum. *Epicutis* (Fig. 222) composed of slender, cylindric hyphae; *pilocystidia* clavate, granular or banded. (Singer 1939: 236.)

R. sordida Pk., Buffalo Soc. Nat. Sci. 1: 57. 1873. *Spores* (Fig. 116) 7.5-8.5 × 6-7.5 μ, warts 0.2 μ or less in height, some isolated, others with fine lines forming an incomplete reticulum. *Epicutis* (Fig. 180) not well developed; cuticle composed of repent hyphae beneath which the hyphae are loosely interwoven and nodulose; no *pilocystidia*. (Singer 1957: 149.)

R. subacris Murr., Torrey Bot. Club Bull. 67: 279. 1940. The following notes are based on a study of a specimen collected and identified by Murrill (Univ. Tenn. Herb. No. 16265): *Spores* (Fig. 126) 8-10.5 × 7-8.5 μ, warts 0.7-1.2 μ high, some catenulate, with a few to many fine lines forming a reticulum. *Epicutis* (Fig. 310) composed of loosely interwoven erect or ascendant hyphae which are cylindric; *pilocystidia* numerous, clavate or subcapitate, more or less granular. (Singer 1957: 232 lists this as a doubtful synonym of *R. emetica* ssp. *lacustris* Singer.)

R. subalbidula Murr., Mycologia 33: 441. 1941. *Spores* (Fig. 115) 8-10 × 7-8 μ, warts 0.6-1.0 μ high, some catenulate, others isolated, with a few fine lines. *Epicutis* (Fig. 164) composed of a turf of erect, slender to broad hyphae, some with ventricose apices; *pilocystidia* slender-clavate, granular to banded. (Singer 1947: 174 says this is not distinguishable from a medium-sized form of *R. anomala* Pk., except that it is usually slightly acrid.)

R. subalutacea Burl., North American Flora 9: 227. 1915. *Spores* (Fig. 110) 9-12 × 7-9 μ, warts 0.6-1.2 μ high, isolated or with a few fine lines. *Pleurocystidia* 63-74 × 6-12 μ, fusoid or ventricose, at times more or less constricted, acute or appendiculate, banded, granular, or empty; *cheilocystidia* 42-70 × 5-10 μ, fusoid or ventricose, at times more or less constricted, acute or rounded, banded, granular, or empty. *Epicutis* (Fig. 230) composed of irregular to somewhat constricted hyphae, 2-5 μ broad, the apices rounded or acute; no *pilocystidia*. (No studies reported by Singer.)

R. subbrunneipes Murr., Florida Acad. Sci. Jour. 8: 182. 1945. *Spores* (Fig. 122) 8.5-10 × 7.5-9 μ, warts 0.7-1.2 μ high, some isolated, others catenulate, with some fine lines. *Pleurocystidia* 58-71 × 6-8 μ, ventricose,

appendiculate, the appendage often disposed at right angles to the long axis, empty or banded; *cheilocystidia* 42-60 × 3-7 μ, clavate, fusoid, cylindric, at times constricted, acute or appendiculate, the appendage at times disposed at right angles to the long axis, empty, granular, or banded. *Epicutis* (Fig. 220) composed of erect to ascendant hyphae, which are slender, the apices tapering or capitate; *pilocystidia* clavate, granular, numerous. (No studies reported by Singer.)

R. subcremeiceps Murr., Lloydia 8: 270. 1945. *Spores* (Fig. 8) 7.5-9 × 6-7 μ, warts 0.1 μ or less in height, many fine lines and some broad bands forming a reticulum. *Pleurocystidia* 55-71 × 6-10 μ, ventricose, appendiculate or capitate, granular or banded; *cheilocystidia* 42-57 × 5-10 μ, ventricose, usually long- or short-appendiculate, banded. *Epicutis* (Fig. 312) composed of more or less nodulose hyphae, the apices tapering or appendiculate; *pilocystidia* clavate, scattered, granular. (No studies reported by Singer.)

R. subdensifolia Murr., Mycologia 33: 441. 1941. The following notes are based on a study of an authentic specimen, No. F 18583, collected and determined by Murrill: *Spores* (Fig. 32) 8.5-10 × 7-8.5 μ, warts 0.7-1.3 μ high, isolated, no fine lines and no bands. *Epicutis* (Fig. 165) composed of a turf of erect, more or less constricted hyphae; *pilocystidia* numerous, clavate, granular to banded. (Singer 1957: 152.)

R. subdepallens Pk., Torrey Bot. Club Bull. 23: 412. 1896. *Spores* (Fig. 20) 8-10 × 7-8.5 μ, warts blunt, stout, 0.6-1.0 μ high, isolated, at times with broad bands. *Pleurocystidia* 50-98 × 6-10 μ, buried or projecting, fusoid to clavate, apices appendiculate, acute, rounded, or capitate; *cheilocystidia* 32-50 × 6-7 μ, fusoid, clavate, acute, appendiculate, or rounded. *Epicutis* (Fig. 231) composed of a zone of gelatinous hyphae with some erect free ends, the apices often acute; no *pilocystidia* found. (No studies reported by Singer.)

R. subflava Murr., Mycologia 33: 442. 1941. *Spores* (Fig. 39) 8-10 × 6-8 μ, warts 0.1-0.3 μ high, fine lines and ridges forming a reticulum. *Pleurocystidia* 48-61 × 7-9 μ, clavate or ventricose, acute to mucronate, granular or banded; *cheilocystidia* 37-43 × 6-10 μ, clavate or ventricose, mucronate, empty or granular. *Epicutis* (Fig. 163) composed of a turf of slender hyphae, which are cylindric to constricted, the apices often acute; *pilocystidia* rather inconspicuous, clavate to spathulate, granular or empty. This species is, of course, not the same as *R. subflava* Singer which Singer, 1957: 152, now places in synonymy with *R. subdensifolia* Murr. (No studies reported by Singer.)

R. subfloridana Murr., Lloydia 8: 271. 1945. *Spores* (Fig. 95) 8-11 × 7-8.5 μ, warts 0.7-1.2 μ high, isolated or short-cantenulate, with some fine lines. *Epicutis* (Fig. 302) composed of a turf of hyphae which are irregularly constricted, some hyphae broad, septate; the apices rounded or acute; no *pilocystidia*. (Singer 1957: 212.)

R. subglauca Murr., Lloydia 6: 217. 1943. *Spores* (Fig. 73) 6.3-8.5 × 4.5-6.3 μ, warts 0.1 μ (rarely 0.2 μ) high, isolated or with a few fine lines. *Epicutis* (Fig. 303) composed of a turf of of septate-constricted hyphae, the terminal elements more or less tapering,—arising from a pseudoparen-

chymatous hypodermium,—the *virescens*-type. (Singer 1957: 194 lists this as a synonym of *R. chlorinosma* Burl.)

R. subgraminicolor Murr., Lloydia 6: 218. 1943. *Spores* (Fig. 157) 7-8.5 × 5.5-7 μ, warts 0.3-0.6 μ high, some isolated, some catenulate, some spores with fine lines. *Pleurocystidia* 46-71 × 5-7 μ, mostly near the lamellae-edges, fusoid to subcylindric, acute or mucronate, slightly granular to banded; *cheilocystidia* 34-44 × 5-8 μ, clavate to fusoid, few, absent in some sections. *Epicutis* (Feb. 313) composed of both narrow, non-septate hyphae, and broader, septate hyphae, the apices more or less acute; no *pilocystidia*. (No studies reported by Singer.)

R. subinconstans Murr., Mycologia 38: 226. 1946. *Spores* (Fig. 88) 6.5-9 × 5.7-7 μ, warts 0.3-0.7 μ high, some isolated, others catenulate, with some fine lines. *Epicutis* (Fig. 317) composed of hyphae which tend to be clavate; no *pilocystidia*. (Singer 1957: 203 lists *R. inconstans* Murr. as a synonym.)

R. subluteobasis Murr., Lloydia 6: 218. 1943. *Spores* (Fig. 47) 10-13 × 9-12 μ, warts 0.9-1.7 μ high, with short ridges and often indistinct fine lines, some isolated. *Epicutis* (Fig. 284) composed of loosely tangled hyphae; *pilocystidia* cylindric to obclavate, banded or with amorphous contents. (Singer 1957: 264.)

R. subobscura Murr., Torrey Bot. Club Bull. 66: 155. 1939. *Spores* (Fig. 136) 8-10.5 × 7-8.2 μ, warts 0.5-1.2 μ high, isolated, at times short-catenulate, no fine lines. *Epicutis* (Fig. 168) composed of a turf of somewhat constricted hyphae, the apices rounded or acute; *pilocystidia* clavate to ventricose, at times subcapitate, granular to banded. (Singer 1957: 153.)

R. subochroleuca Murr., Mycologia 30: 363. 1938. *Spores* (Fig. 154) 8-10 × 6.5-8 μ, warts usually less than 0.1 μ high, with fine lines and some broad bands. *Epicutis* (Fig. 187) composed of a turf of hyphae; no *pilocystidia*. (Singer 1957: 191 lists this as a synonym of *R. ochroleucoides* Kauff.)

R. subochrophylla Murr., Mycologia 39: 364. 1938. *Spores* (Fig. 155) 8-10 × 5.5-7.5 μ, warts 0.2-0.5 μ high, with some fine lines and broad bands. *Pleurocystidia* 51-62 × 8-10 μ, few and inconspicuous, ventricose, appendiculate, empty or granular; *cheilocystidia* 43-52 × 7-10 μ, clavate or ventricose, at times constricted, appendiculate, empty or banded. *Epicutis* (Fig. 261) composed of a loose turf of hyphae which are often irregularly constricted; no *pilocystidia*. (No studies reported by Singer.)

R. subpavonina Murr., Lloydia 8: 271. 1945. *Spores* (Fig. 17) 9-11 × 8-9 μ, warts numerous, cylindric, 0.8-1.2 μ high, some isolated, others catenulate, with a few fine lines. *Pleurocystidia* 50-74 × 8-11 μ, ventricose, mucronate, acute, or capitate, banded; *cheilocystidia* 52-61 × 7-9 μ, ventricose, acute to appendiculate-capitate, granular or banded. *Epicutis* (Fig. 219) composed of a loose turf of hyphae which are more or less constricted; *pilocystidia* clavate, granular to minutely banded. (No studies reported by Singer.)

R. subpruinosa Murr., Lloydia 7: 313. 1944. *Spores* (Fig. 15) 8-11 × 7-9 μ, warts 0.4-0.6 μ high, isolated, most of the spores with a few indistinct, fine lines. *Pleurocystidia* 41-56 × 6-11 μ, ventricose, fusoid, or

clavate, acute or appendiculate, empty or granular; *cheilocystidia* 37-52 × 7-12 μ, numerous, clustered, ventricose, acute or appendiculate, empty. *Epicutis* (Fig. 203) composed of a turf of hyphae which are cylindric to ventricose or constricted, the apices tapering or rounded. (No studies reported by Singer.)

R. subpusilla Murr., Mycologia 33: 285. 1941. *Spores* (Fig. 124) 7.5-9 × (6.3) 7-8 μ, warts 0.8-1.4 μ high, some isolated, a few fine lines and broad bands forming an incomplete reticulum. *Pleurocystidia* 48-60 × 6-9 μ, clavate, at times constricted, subcapitate, mucronate, or appendiculate, empty or banded; *cheilocystidia* 28-42 × 5-8 μ, cylindric to clavate, some mucronate, others rounded, granular or banded. *Epicutis* (Fig. 169) composed of a turf of more or less nodulose hyphae, the apices rounded, at times appendiculate; *pilocystidia* clavate, at times appendiculate, granular to banded. (No studies reported by Singer.)

R. subrubescens Murr., Torrey Bot. Club Bull. 67: 146. 1940. *Spores* (Fig. 108) 9-11 × 8-9.5 μ, warts 1.0-1.4 μ high, isolated to short-catenulate, no fine lines. *Pleurocystidia* 45-68 × (6) 8-12 μ, fusoid or clavate, at times appendiculate or mucronate, empty, granular or banded; *cheilocystidia* 28-51 × 4-7 μ, cylindric, clavate, or ventricose, empty, granular, or minutely banded. *Epicutis* (Fig. 170) composed of a turf of hyphae which are cylindric to nodulose-constricted; *pilocystidia* clavate, the apices acute or rounded, minutely banded. (No studies reported by Singer.)

R. subsericeonitens Murr., Torrey Bot. Club Bull. 66: 156. 1939. *Spores* (Fig. 117) 8-9.5 × 7.5-8 μ, warts 0.6-1.0 μ high, usually broad and blunt, isolated or with a few fine lines. *Epicutis* (Fig. 215) composed of slender, clavate hyphae, the apices rounded; *pilocystidia* numerous, slender-clavate, granular. (Singer 1957: 151.)

R. subsordida Pk., New York State Mus. Bull. 105: 40. 1906. *Spores* (Fig. 76) 7-8.5 × 5.6-7 μ, warts 0.2 μ high or less, some isolated, with a few short ridges and fine lines. *Epicutis* (Fig. 246) not differentiated or only slightly so; the *cuticle* composed of repent surface hyphae, or with a few more or less erect hyphae; most of the hyphae beneath surface with inflated cells; no *pilocystidia*. It appears that *R. subsordida* Pk. is a synonym of *R. sordida* Pk. which in turn is a synonym of *R. albonigra* (Kromb.) Fr. (For studies on *R. albonigra*, see Singer 1957: 149.)

R. subsulphurea Murr., Florida Acad. Sci. Jour. 8: 183. 1945. *Spores* (Fig. 159) 7-8.5 × 5.7-7 μ, warts 0.1-0.3 μ high, broad bands and fine lines forming a reticulum. *Pleurocystidia* 48-76 × 4-7 (11) μ, fusoid, ventricose, or cylindric, acute or appendiculate, empty or banded; *cheilocystidia* 38-53 × 4-8 μ, fusoid or cylindric, apex rounded, acute, or appendiculate. *Epicutis* (Fig. 314) composed of erect to ascendant hyphae which are more or less nodulose-constricted, the apices acute; no *pilocystidia*. (No studies reported by Singer.)

R. subvariata Murr., Lloydia 7: 314. 1944. *Spores* (Fig. 89) 8-10.5 × 7-9 μ, warts 0.9-1.3 μ high, isolated or with a few fine lines which at times form an incomplete reticulum. *Pleurocystidia* 60-73 × 9-11 μ, ventricose, capitate or button-like, or appendiculate, granular or banded; *cheilocystidia* 40-50 × 7-9 μ, ventricose, acute or appendiculate, granular or banded. *Epicutis* (Fig. 167) composed of erect or ascendant hyphae which are cylindric to nodulose-constricted, the apices at times appendicu-

late; *pilocystidia* numerous, cylindric to nodulose-constricted, granular, the apices acute, rounded, or subcapitate. (No studies reported by Singer.)

R. tennesseensis Singer, Soc. Myc. Fr. Bull. 55: 229. 1939. The following notes are based on a study of University of Tennessee collection No. 11496, a part of the collection sent by the writer to Singer: *Spores* (Fig. 59) 6-8 × 7.3-7 μ, warts 0.4-0.5 μ high, a few catenulate, both fine lines and broad bands forming a reticulum. *Epicutis* (Fig. 178) composed of erect to repent brownish hyphae, with a few lactifers; the *hypodermium* composed of a lattice of narrow hyphae. No *pilocystidia*. (Singer 1939: 229.)

R. tenuiceps Kauff., Mich. Acad. Sci. Rept. 11: 81. 1909. *Spores* (Fig. 71) 8-9.5 × 6.3-8 μ, warts 0.5-0.8 μ high, some isolated, others catenulate, with a few fine lines forming a reticulum. *Epicutis* (Fig. 226) composed of nodulose-constricted to cylindric hyphae, the apices rounded or acute; *pilocystidia* rather numerous, slender to broadly clavate, minutely banded. (Singer 1957: 259.)

R. testaceiceps Murr., Lloydia 8: 272. 1945. *Spores* (Fig. 138) 7-8.5 × 6-7 μ, warts 0.4-0.8 μ high, isolated, with some fine lines. *Epicutis* (Fig. 166) composed of a turf of cylindric to nodulose-constricted hyphae, the apices rounded to appendiculate; *pilocystidia* few, inconspicuous, clavate, only slightly granular. (Singer 1957: 262 lists this as a synonym of *R. praefragilis* Murr., but there are differences in the epicutis of the types.)

R. tuberculata Murr., Torrey Bot. Club Bull. 67: 58. 1940. *Spores* (Fig. 24) 8.5-12 × 8-10 μ, warts 0.8-1.5 μ high, stout, several broad bands and a few fine lines forming a reticulum. *Epicutis* (Fig. 205) composed of scattered hyphae of two types: (1) slender, constricted, non-septate, and (2) strongly constricted, septate, broader hyphae,—at times appearing as a chain of elements, the apices somewhat acute; no *pilocystidia*. (Singer 1957: 187.)

R. uncialis Pk., New York State Mus. Bull. 1 (No. 2): 10. 1887. *Spores* (Fig. 139) 7.5-9 × 5.5-7 μ, warts mostly 1.0 μ or less in height, occasionally up to 0.3 μ high, at times short-catenulate, often isolated, a few fine lines. *Pleurocystidia* 66-90 × 7-9 μ, clavate to ventricose, at times constricted, acute to subcapitate, at times mucronate, banded; *cheilocystidia* 36-52 × 7-9 μ, ventricose, acute, mucronate, or appendiculate, banded or empty. *Epicutis* (Fig. 269) composed of a turf of irregular, often nodulose hyphae, arising from a hypodermium which is apparently pseudoparenchymatic, approaching the *virescens*-type. (No studies reported by Singer.)

R. uncialiformis Murr., Lloydia 6: 219. 1943. *Spores* (Fig. 99) 8-10 × 7-8.5 μ, warts 0.8-1.3 μ high, some isolated, some catenulate, with some fine lines. *Pleurocystidia* 36-63 × 5-9 μ, clavate or obclavate, mucronate, empty; *cheilocystidia* 38-50 × 6-10 μ, clavate, ventricose, mucronate, empty. *Epicutis* (Fig. 216) composed of erect, more or less nodulose hyphae, the apices at times slightly appendiculate; *pilocystidia* several to numerous, few or none in oldest carpophores. (No studies reported by Singer.)

R. variata Banm., Bot. Gaz. 5: 165. 1881. The following notes are based on a study of specimens marked "type," but there is now a note written by a later hand that the collection is not acceptable as the type: *Spores* (Fig. 37) 8-10 (12) × 6-9 μ, often more or less inequilateral, warts acute and slender, 0.4-1.0 μ high, isolated or catenulate, at times with fine

lines. *Epicutis* (Fig. 298) composed of erect or ascendant hyphae, cylindric to fusoid, at times appendiculate; *pilocystidia*-like elements present, granular or banded. (Singer 1957: 170.)

R. variegata Singer, Sydowia 11: 186. 1957. *Spores* (Fig. 151) 6.3-8.5 × 5-6.5 μ, warts 0.3-0.6 μ high, with broad bands and fine lines forming a partial reticulum. *Epicutis* (Fig. 211) composed of septate-constricted hyphae in pyramidal tufts, the terminal elements acute or rounded, the basal elements appearing as a chain of cells; between the tufts the surface hyphae are repent. *Pilocystidia* none.

R. variicolor Murr., Lloydia 6: 219. 1943. *Spores* (Fig. 158) 7-9 × 6.3-8 μ, warts 0.8-1.0 μ high, isolated, some broad bands and fine lines forming an incomplete reticulum. *Epicutis* (Fig. 287) composed of a trichodermial septate hyphae, some terminal elements rounded, others acute, at times the basal elements as sphaerocysts; no *pilocystidia*. (Singer 1957: 189.)

R. ventricosipes Pk., Torrey Bot. Club Bull. 29: 70. 1902. *Spores* (Fig. 5) (6) 7-8 (11) × 4.5-6 μ, warts 0.1 μ or less in height, at times apparently absent, fine lines several, few, or none. *Epicutis* (Fig. 179) not differentiated; the cuticle composed of repent hyphae, or with an occasional erect hypha; some hyphae below the surface are cystidia-like. (Singer 1942: 69.)

R. venusta Murr., Lloydia 8: 272. 1945. *Spores* (Fig. 107) 7.5-11 × 7-9 μ, warts 0.7-1.2 μ high, isolated, at times short-catenulate. *Pleurocystidia* 45-96 × 7-10 μ, prominent, versiform: fusoid, ventricose, clavate, to cylindric, arising deep in the gill-trama, rounded or acute, at times capitate, or mucronate, granular or banded; *cheilocystidia* 37-76 × 7-10 μ, prominent, clavate-cylindric, or more rarely ventricose, empty, granular, or banded. *Epicutis* (Fig. 171) composed of a turf of numerous slender hyphae, the apices usually acute; *pilocystidia* clavate, often pale yellowish, granular to minutely banded. (No studies reported by Singer.)

R. vesicatoria Burl., Mycologia 36: 118. 1944. *Spores* (Fig. 93) 7.5-10 × 6-8 μ, warts 0.4-0.7 μ high, isolated or catenulate, fine lines forming an incomplete reticulum. *Epicutis* (Fig. 208) composed of a palisade of slender hyphae, and some scattered hyphae; with occasional buried *pilocystidia*. (Singer 1957: 145.)

R. vinacea Burl., North American Flora 9: 217. 1915. The following notes are based on a specimen, No. 97-1912, determined by Burlingham: *Spores* (Fig. 11) 9-10.5 × 7.5-9 μ, warts 0.9-1.2 μ high, isolated or short-catenulate, fine lines forming a more or less complete reticulum. *Epicutis* (Fig. 213) composed of erect hyphae which are cylindric, clavate, or subfusoid, the apices rounded or subacute; *pilocystidia* clavate, banded, conspicuous. (Singer 1942: 83.)

R. vinosirosea Murr., Lloydia 6: 219. 1943. *Spores* (Fig. 148) 7-9 × 5.7-7.5 μ, warts 0.3-0.5 μ high, isolated, at times catenulate, many spores with fine lines which form an incomplete reticulum. *Pleurocystidia* scattered, 38-50 × 6-7 μ, ventricose to fusoid, appendiculate, empty, granular, or banded; *cheilocystidia* 30-43 × 5-9 μ, few, ventricose, appendiculate or mucronate, empty or granular. *Epicutis* (Fig. 316) composed of loosely-disposed, erect, somewhat nodulose hyphae, the apices acute; *pilocystidia* cylindric to constricted, or subfusoid. (No studies reported by Singer.)

R. viridella Pk., New York State Mus. Bull. 105: 41. 1906. *Spores* (Fig. 133) 6-7.2 × 5-5.8 μ, warts 0.2-0.3 μ high, with a few fine lines not forming a complete reticulum. *Epicutis* (Fig. 227) composed of cylindric to nodulose hyphae, the apices rounded or slightly acute; *pilocystidia* cylindric, ventricose, or constricted, at times appendiculate, minutely banded to nearly empty; the epicuticular hyphae and pilocystidia occur at intervals as mounds over the lepidote surface, and between these mounds the cuticular hyphae are repent. (Singer 1942: 72.)

R. watsoniana Murr., Torrey Bot. Club Bull. 66: 156. 1939. *Spores* (Fig. 18) 9-12 × 7-8.5 μ, warts 0.8-1.3 μ high, isolated or catenulate, with a few fine lines. *Pleurocystidia* 61-96 × 6-12 μ, numerous, conspicuous, ventricose to irregularly-cylindric or constricted, apices acute or appendiculate, granular or banded; *cheilocystidia* few, 42-50 × 5-8 μ, ventricose to subcylindric, acute or appendiculate, granular. *Epicutis* (Fig. 191) not well developed; the cuticle composed of repent hyphae with scattered, at times numerous, ascendant or erect hyphae, the apices rounded to subcapitate, or acute; no *pilocystidia*. (No studies reported by Singer.)

R. westii Murr., Mycologia 33: 443. 1941. *Spores* (Fig. 4) 7-9 × 5-6.3 μ, warts rarely more than 0.1 μ high, often mere punctations, at times catenulate, with a few fine lines. *Epicutis* (Fig. 192) composed of cylindric to nodulose, erect hyphae; no *pilocystidia*. (Singer 1957: 199 reports findings ornamentations up to 0.7 μ high.)

R. xerampelina var. **semirubra** Singer, Sydowia 11: 218. 1957. The following notes are based on an authentic specimen determined by Singer, collected near West Roxbury, Massachusetts, August 30, 1945: *Spores* (Fig. 19) 9-11 × 7-9 μ, warts 0.8-1.6 μ high, isolated, with a few fine lines. *Epicutis* (Fig. 305) composed of hyphal tufts, the hyphae slender-cylindric or broad and the terminal elements subulate; *pilocystidia* clavate, granular.

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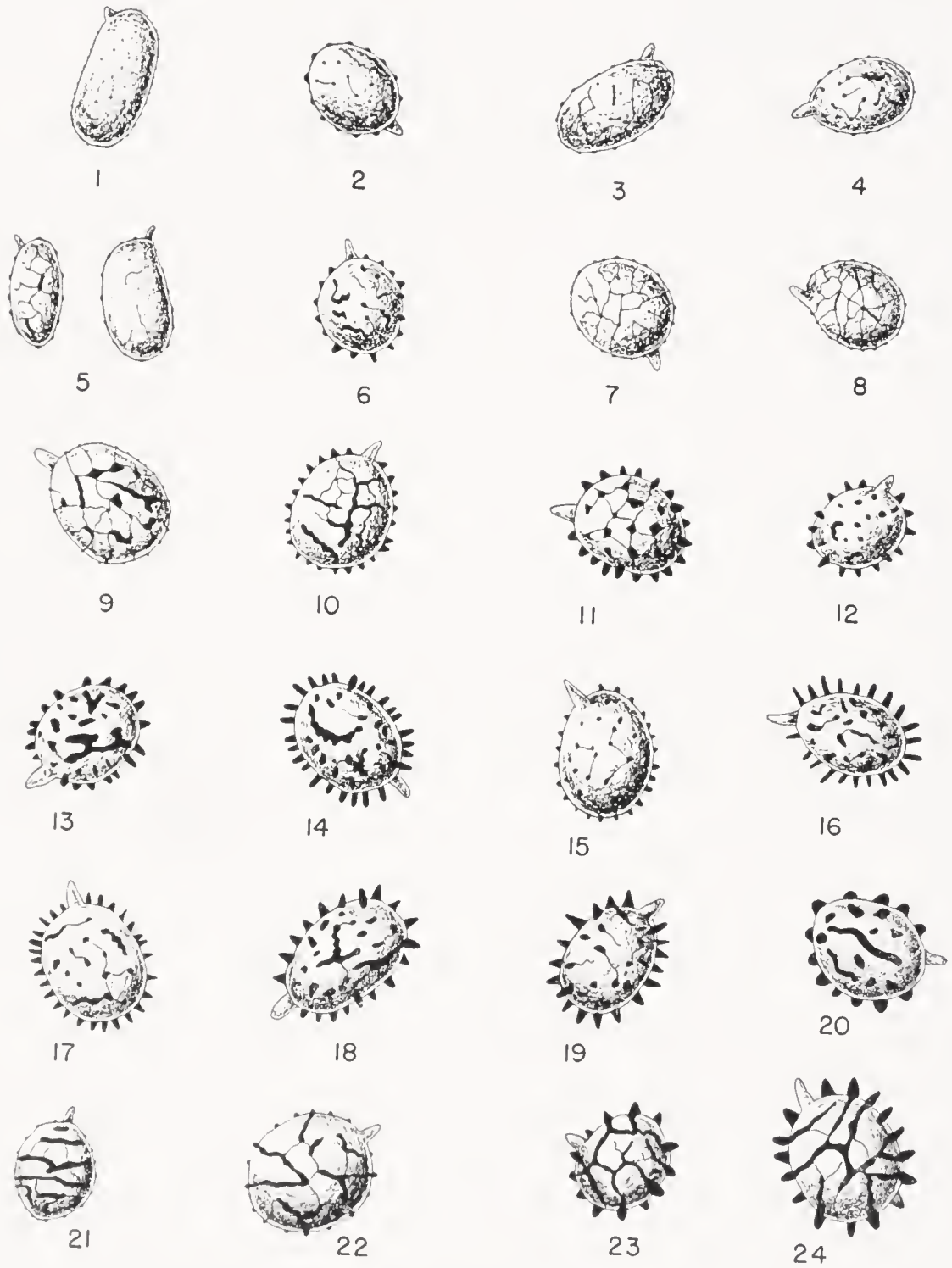
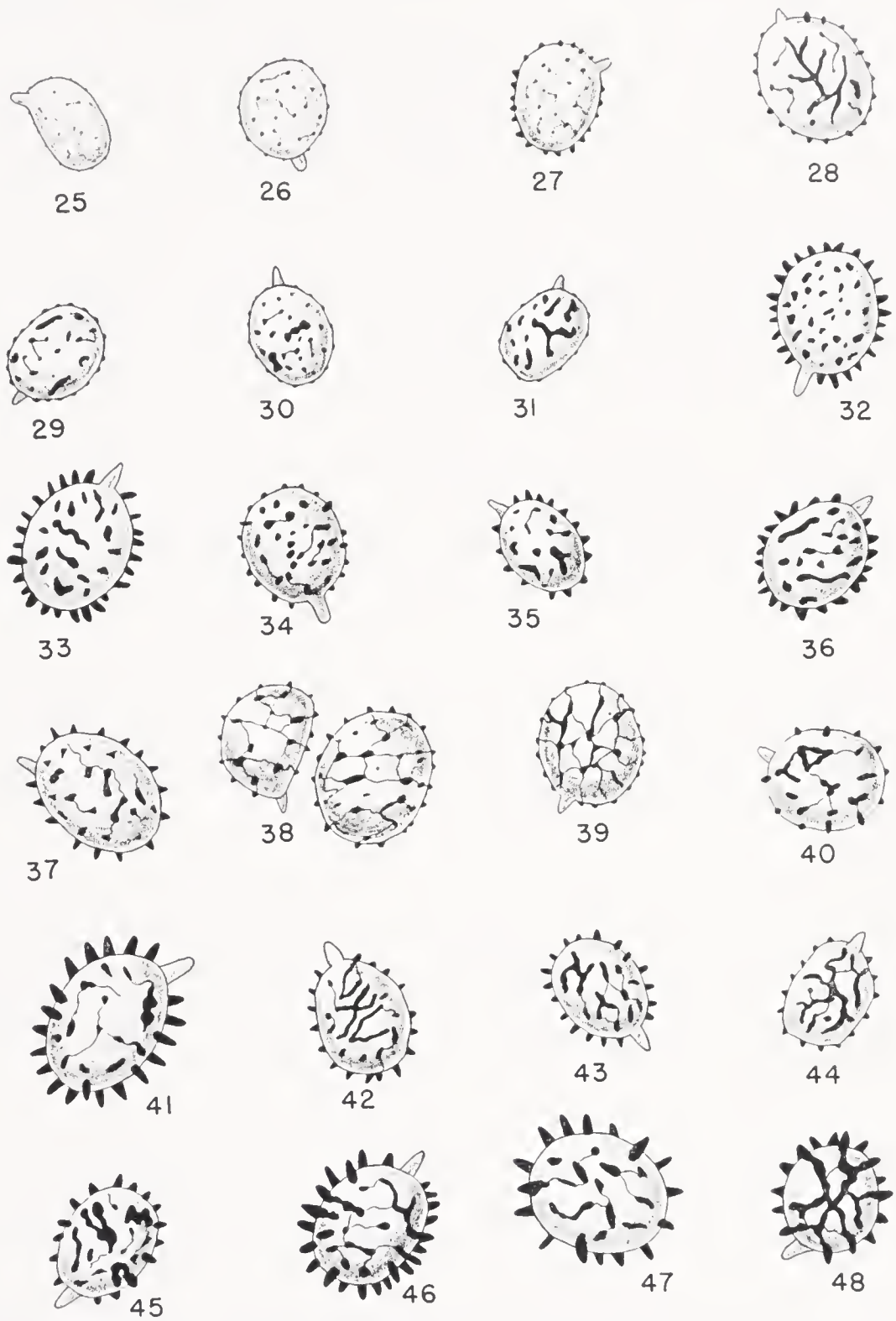
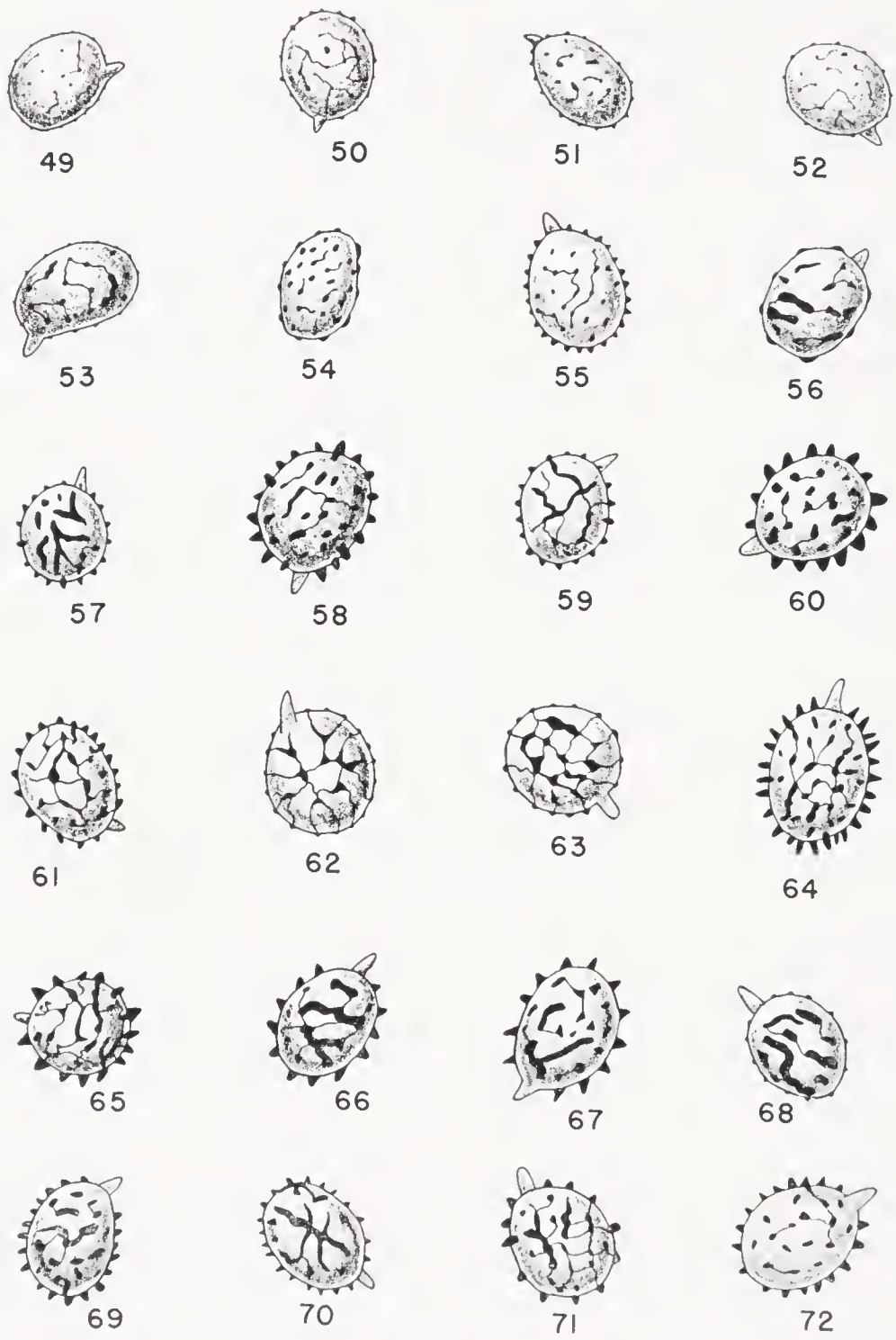


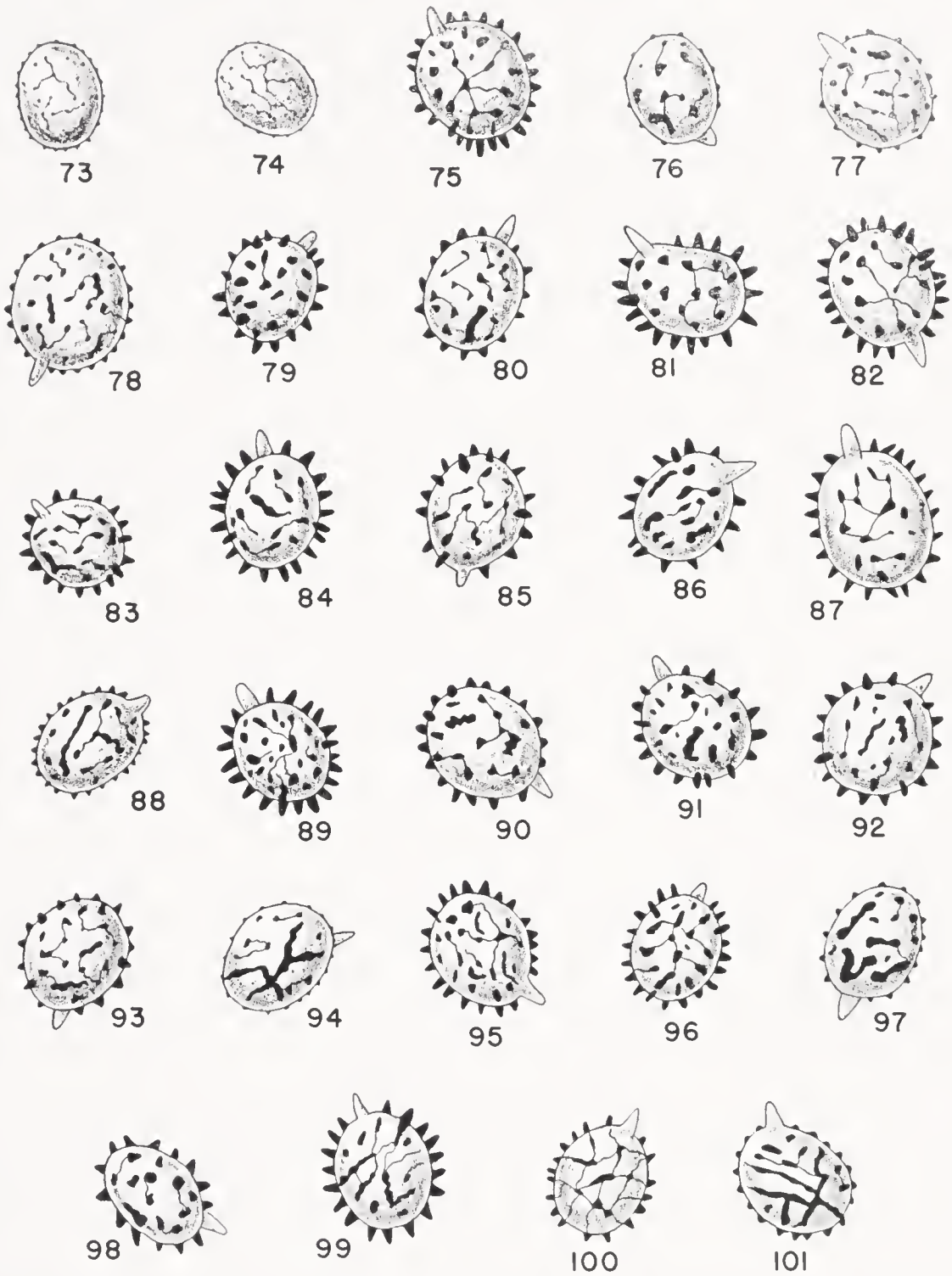
Russula spores: Fig. 1. *heterospora* Beards., 2. *affinis* Burl., 3. *beardslei* Burl., 4. *weslii* Murr., 5. *ventricosipes* Pk., 6. *admirabilis* Burl., 7. *burkei* Burl., 8. *suberemicoeps* Murr., 9. *ochroleucoides* Kauff., 10. *rubrifolia* Murr., 11. *vinacea* Burl., 12. *leucomodesta* Sing., 13. *albiflavescens* Murr., 14. *albiclaripes* Murr., 15. *subpruinosa* Murr., 16. *perplexa* Burl., 17. *subpavonina* Murr., 18. *watsoniana* Murr., 19. *xerampelina* var. *semirubra* Sing., 20. *subdepallens* Pk., 21. *ochroleuciformis* Murr., 22. *magna* Beards., 23. *alachuana* Murr., 24. *tuberculata* Murr.



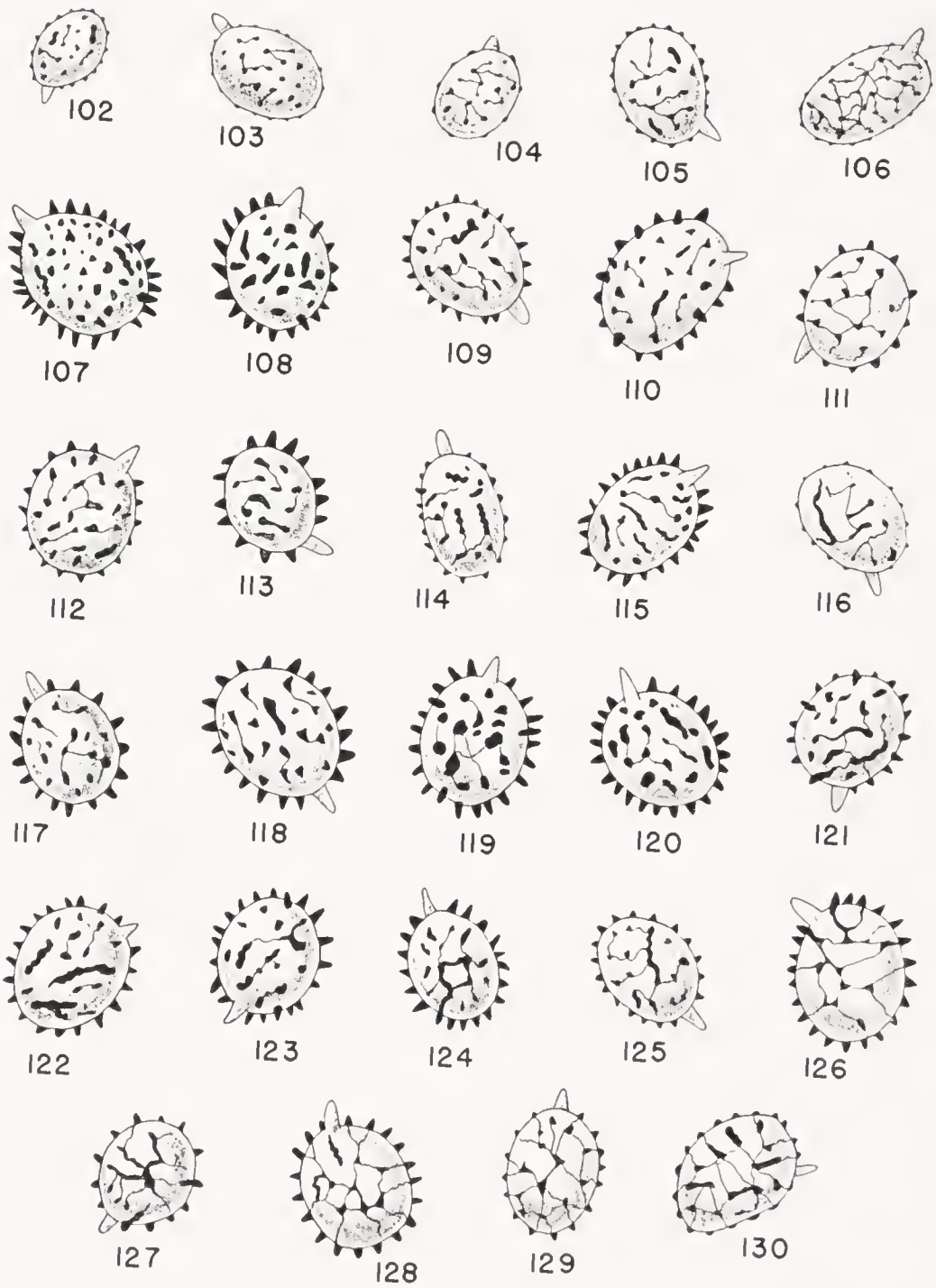
Russula spores: Fig. 25. *heterosporoides* Murr., 26. *albiduliformis* Murr., 27. *appalachiensis* Sing., 28. *inedulis* Murr., 29. *crustosa* Pk., 30. *brunneola* Burl., 31. *basifurcata* Pk., 32. *subdensifolia* Murr., 33. *arnoldae* Murr., 34. *ferrotineta* Sing., 35. *granulata* Pk., 36. *anomala* Pk., 37. *variata* Bann., 38. *balloui* Pk., 39. *subflava* Murr., 40. *blackfordae* Pk., 41. *hixsoni* Murr., 42. *australirosea* Murr., 43. *alutaceiformis* Murr., 44. *luteispora* Murr., 45. *amygdaloides* Kauff., 46. *cystidiosa* Murr., 47. *sublutcobasis* Murr., 48. *granulosula* Murr.



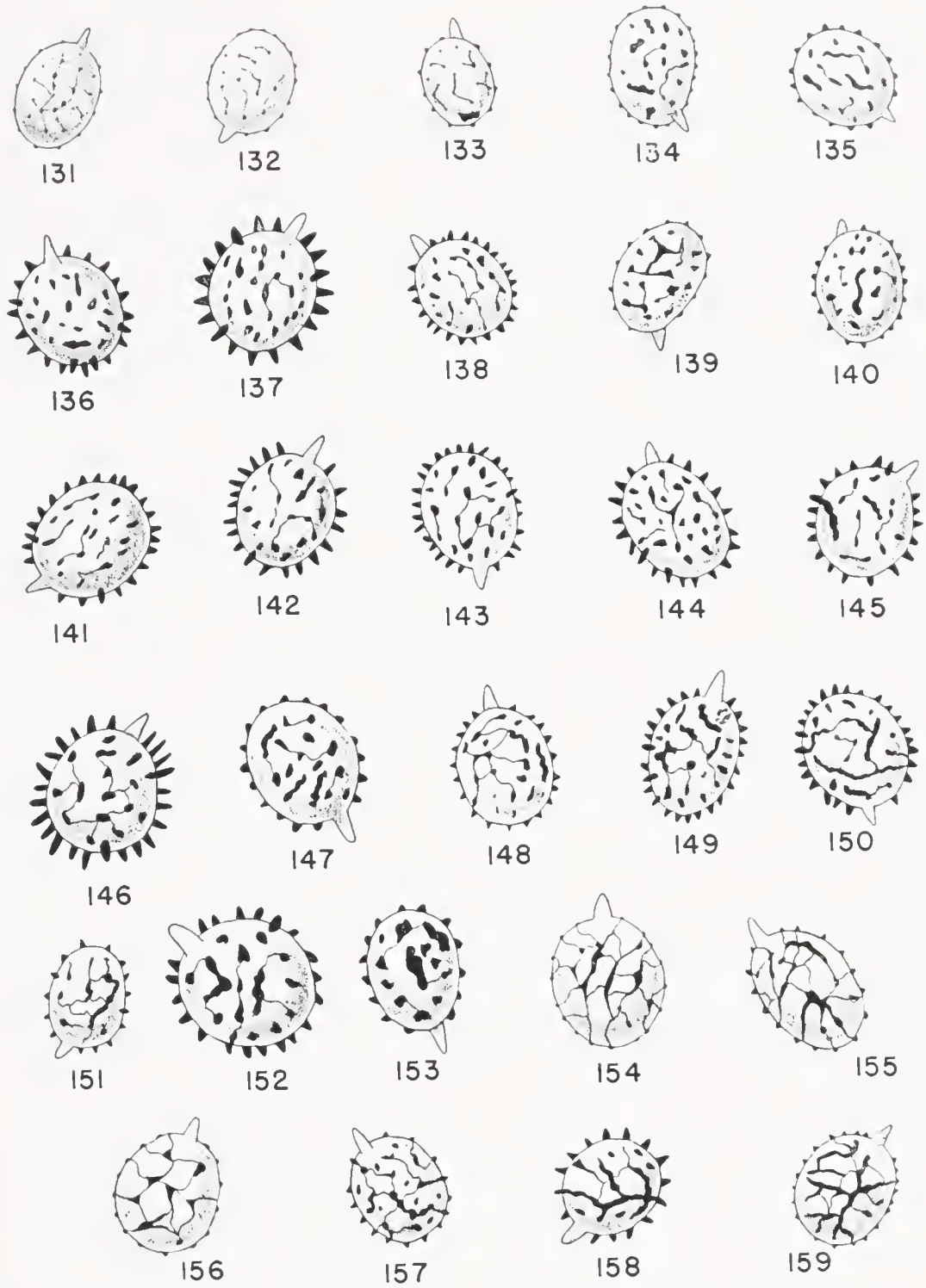
Russula spores: Fig. 49. *chlorinosma* Burl., 50. *rubripurpurea* Murr., 51. *glauca* Burl., 52. *floccnlosa* Burl., 53. *novispora* Murr., 54. *magnifica* Pk., 55. *pseudofoetens* Murr., 56. *rugulosa* Pk., 57. *albidicremea* Murr., 58. *aurantialutea* Kauff., 59. *tennescensis* Sing., 60. *mutabilis* Murr., 61. *pectinatoides* Pk., 62. *lutescentifolia* Murr., 63. *compacta* Frost & Pk., 64. *incarnaticeps* Murr., 65. *mariae* Pk., 66. *lutobasis* Pk., 67. *foetentula* Pk., 68. *flavida* Pk., 69. *albella* Pk., 70. *nigrescentipes* Pk., 71. *tenuiceps* Kauff., 72. *pseudolepida* Sing.



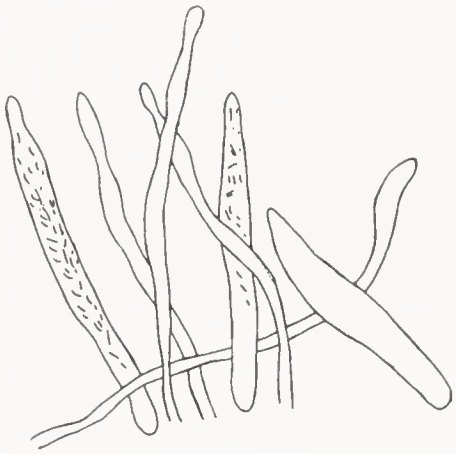
Russula spores: Fig. 73. *subglauca* Murr., 74. *rosei-isabellina* Murr., 75. *emeticiformis* Murr., 76. *subsordida* Pk., 77. *sericella* Murr., 78. *patriotica* Murr., 79. *sericeonitens* Kauff., 80. *palustris* Pk., 81. *pinetorum* Murr., 82. *pinicola* Murr., 83. *glaucescentipes* Murr., 84. *furcatifolia* Murr., 85. *pulchra* Burl., 86. *mutantipes* Murr., 87. *regalis* Murr., 88. *subinconstans* Murr., 89. *subvariata* Murr., 90. *cratacgorum* Murr., 91. *borealis* Kauff., 92. *serissima* Pk., 93. *vesicatoria* Burl., 94. *partirosea* Murr., 95. *subfloridana* Murr., 96. *albida* Pk., 97. *albidula* Pk., 98. *atropurpurea* Pk., 99. *uncialiformis* Murr., 100. *fragilioides* Murr., 101. *eremeirubra* Murr.



Russula spores: Fig. 102. *carlei* Pk., 103. *corallina* Burl., 104. *eccentrica* Pk., 105. *cinerascens* Beards., 106. *cremea* (Murr.) Sing., 107. *venusta* Murr., 108. *subrubescens* Murr., 109. *floridana* Murr., 110. *subalutacea* Burl., 111. *similima* Pk., 112. *brunnicipes* Murr., 113. *brevipes* Pk., 114. *anisata* Murr., 115. *subalbidula* Murr., 116. *sordida* Pk., 117. *subsericeonitens* Murr., 118. *pungens* Beards., 119. *praerubra* Murr., 120. *pinophila* Murr., 121. *diaboli* Sing., 122. *subbrunnicipes* Murr., 123. *pusilliformis* Murr., 124. *subpusilla* Murr., 125. *pusilla* Pk., 126. *subacris* Murr., 127. *viridirosea* Murr., 128. *pervirginea* Murr., 129. *peckii* Sing., 130. *nigrodisca* Pk.



Russula spores: Fig. 131. *rimosa* Murr., 132. *maculosa* Murr., 133. *viridella* Pk., 134. *fosteriana* Murr., 135. *praetenuis* Murr., 136. *subobscura* Murr., 137. *cremeirosea* Murr., 138. *testaceiceps* Murr., 139. *uncialis* Pk., 140. *modesta* Pk., 141. *praerubriceps* Murr., 142. *praeclavipes* Murr., 143. *praecompacta* Murr., 144. *roseilineta* Murr., 145. *macropoda* Sing., 146. *perlactea* Murr., 147. *ochrophylla* Pk., 148. *vinosirosea* Murr., 149. *albimarginata* Murr., 150. *obscuriformis* Murr., 151. *variegata* Sing., 152. *levyana* Murr., 153. *flaviceps* Pk., 154. *subochroleuca* Murr., 155. *subochrophylla* Murr., 156. *levispora* Murr., 157. *subgraminicolor* Murr., 158. *variicolor* Murr., 159. *subsulphurea* Murr.

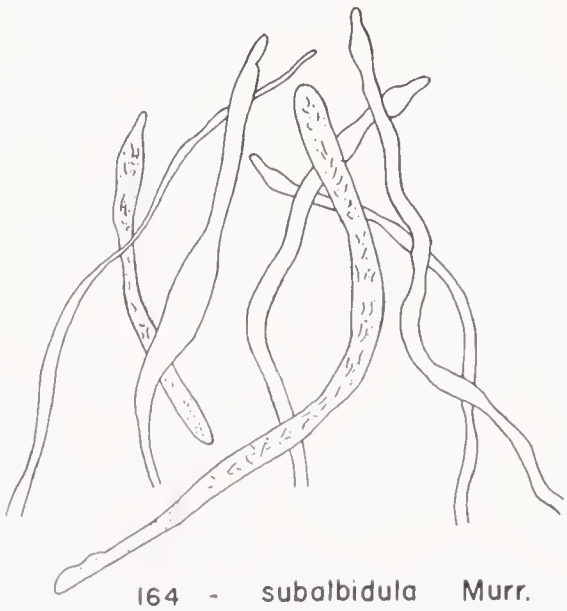


160 - praeclavipes Murr.

161 - praerubriceps Murr.

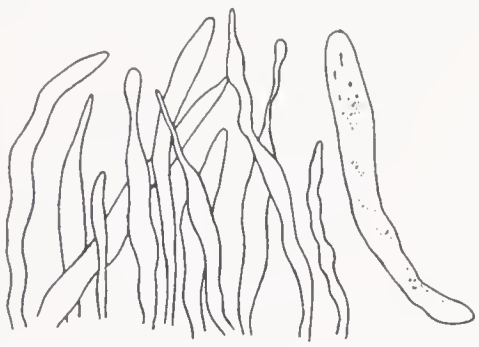
162 - pseudofoetens Murr.

163 - subflava Murr.

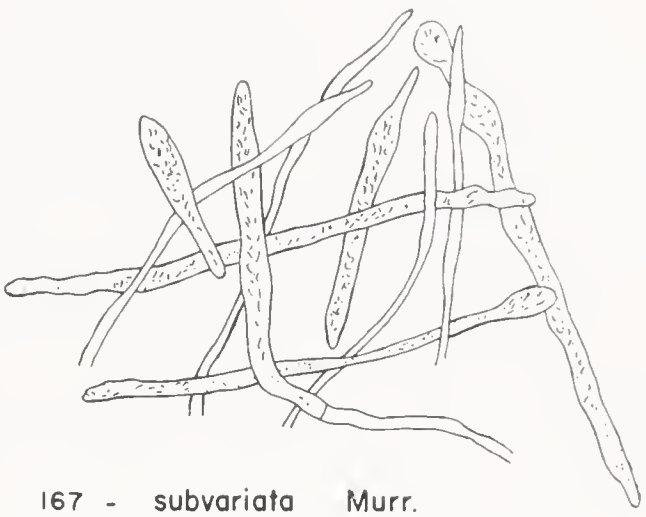


164 - subalbidula Murr.

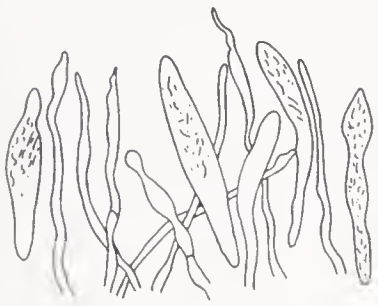
165 - subdensifolia Murr.



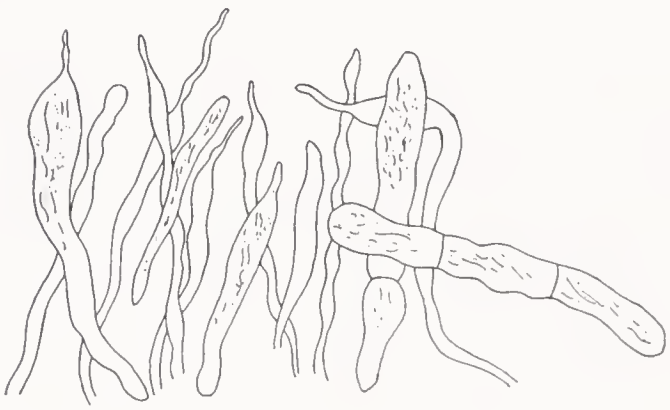
166 - testaceiceps Murr.



167 - subvariata Murr.

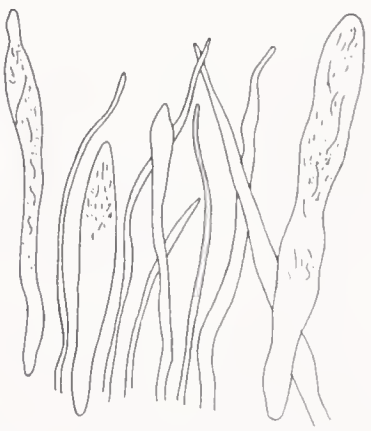


168 - subobscura Murr.

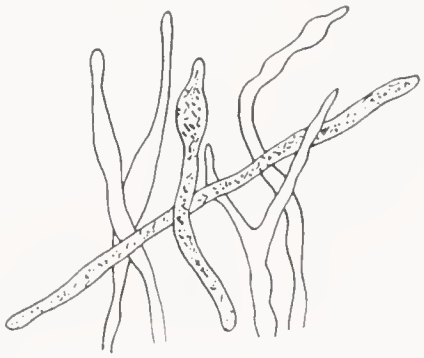


169 - subpusilla Murr.

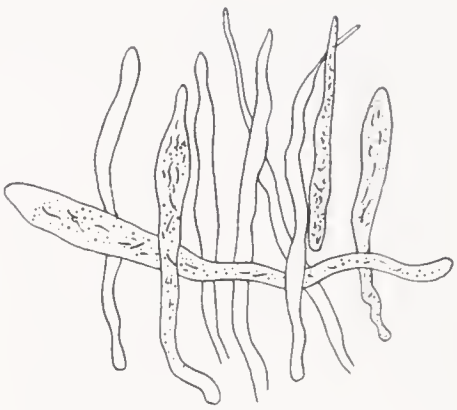
170 - subrubescens Murr.



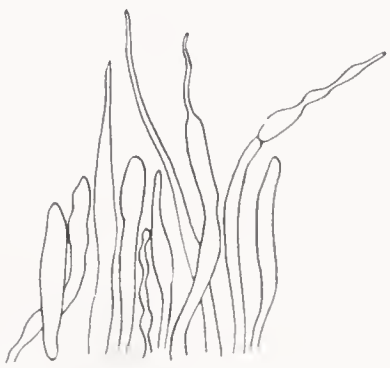
171 - venusta Murr.



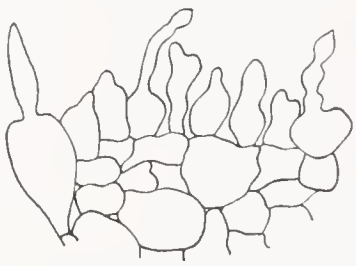
172 - brunneipes Murr.



173 - fragilioides Murr.

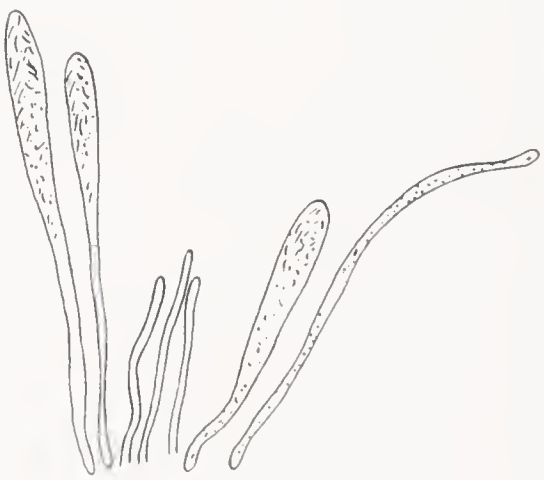


174 - lutescentifolia Murr.

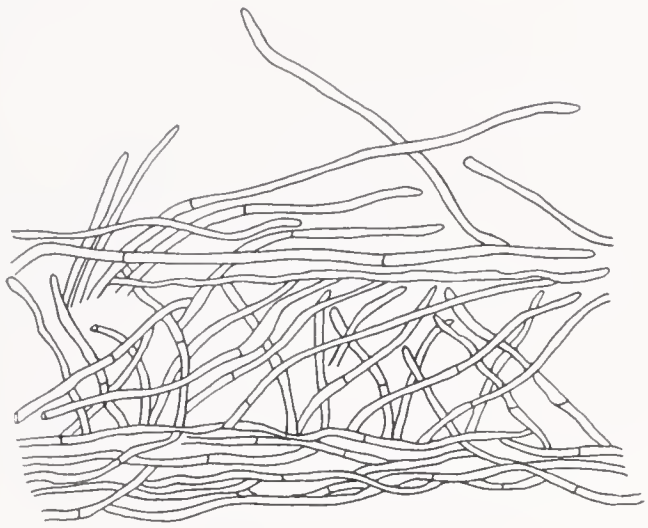


175 - heterosporoides Murr.

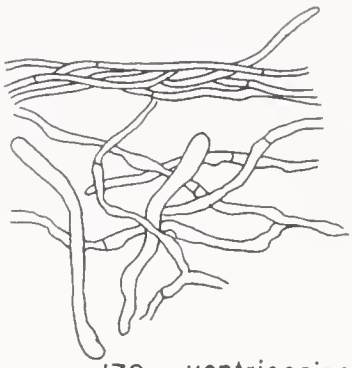
176 - levispora Murr.



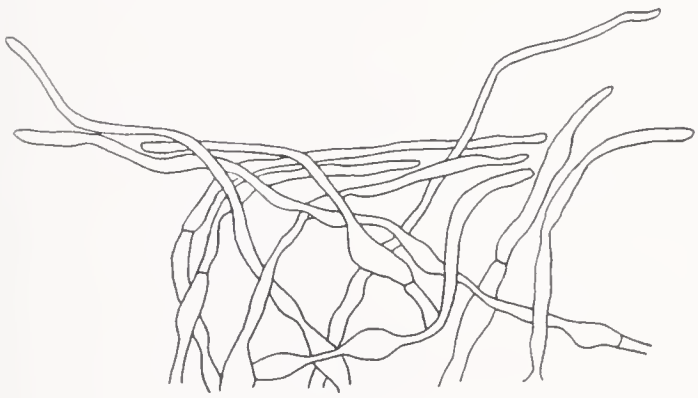
177 - partirosea Murr.



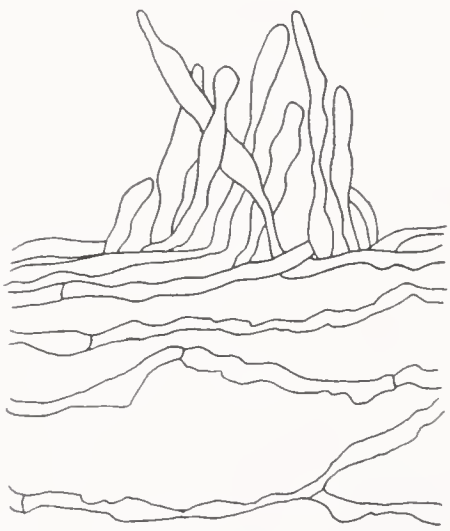
178 - tennesseensis Sing.



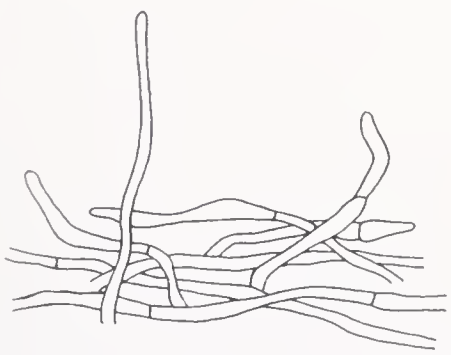
179 - ventricosipes Pk.



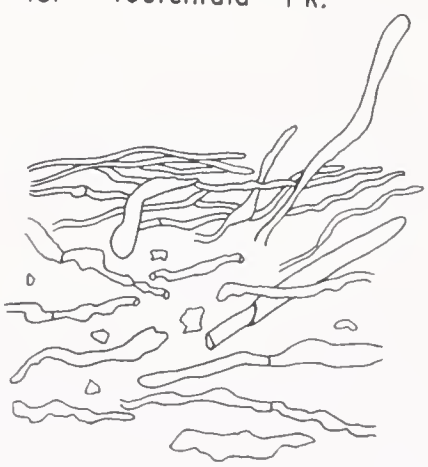
180 - sordida Pk.



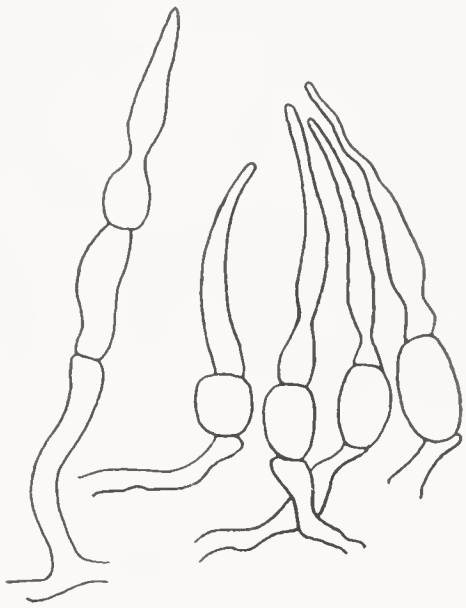
181 - foetentula Pk.



182 - eccentrica Pk.

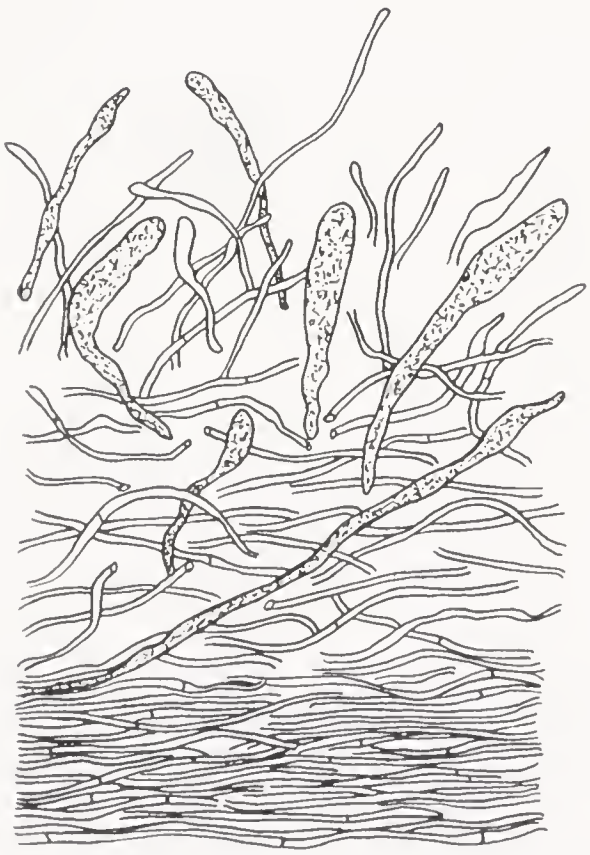


183 - heterospora Beards.

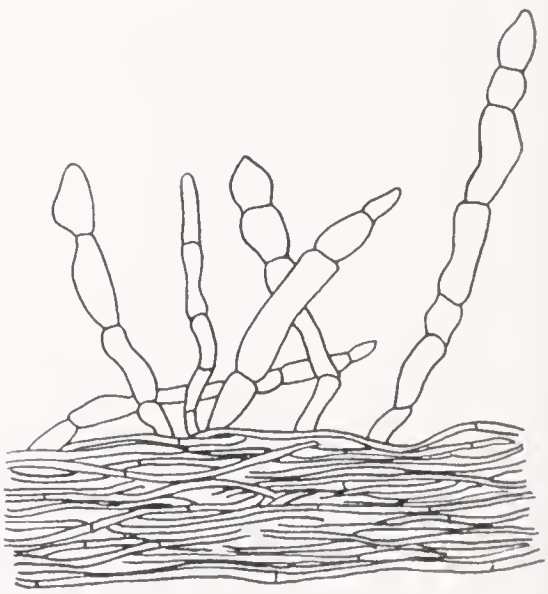


184 - alachuana Murr.

185 - affinis Burl.



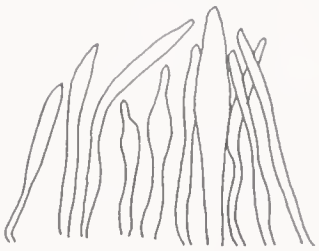
a in youth



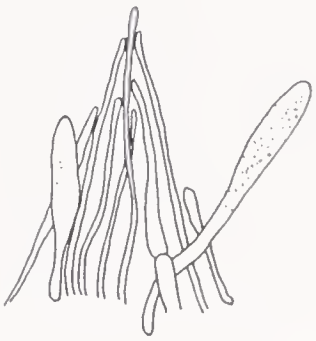
b in age

186 - albella Pk.

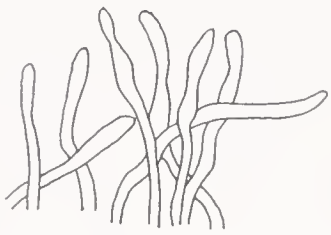
187 - subochroleuca Murr.



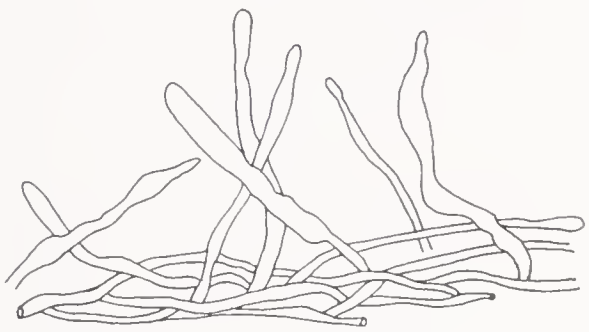
188 - ochroleucoides Kauff.



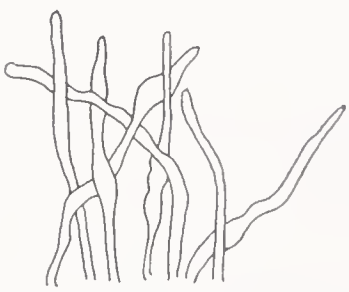
189 - floridana Murr.



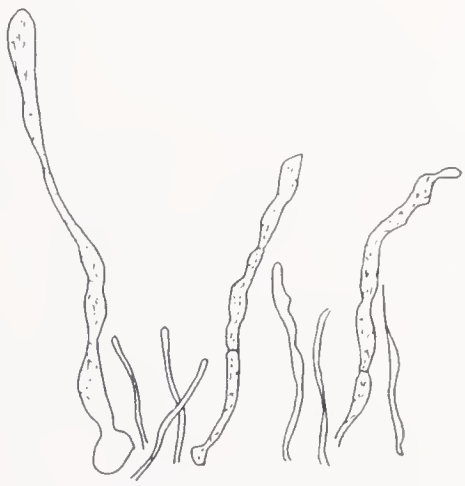
190 - ochroleuciformis Murr.



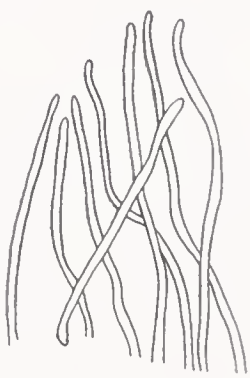
191 - watsoniana Murr.



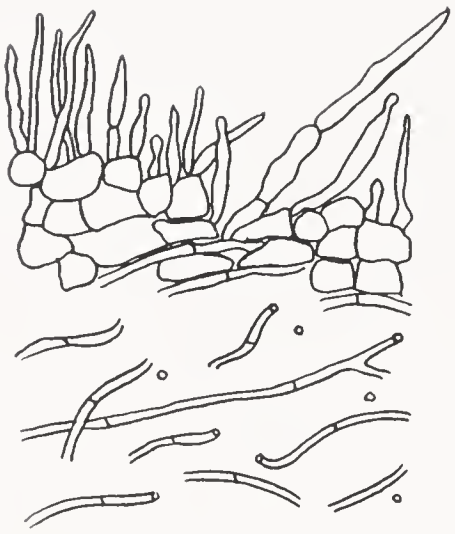
192 - westi Murr.



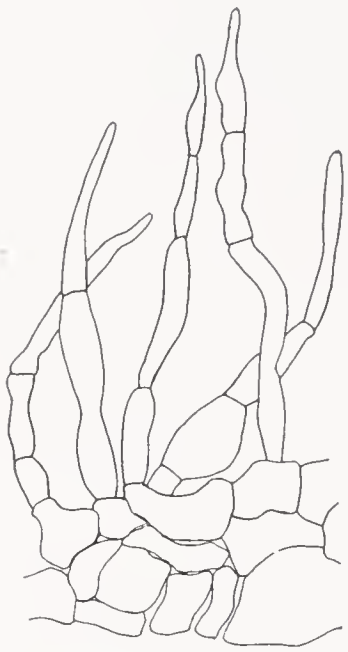
193 - anisata Murr.



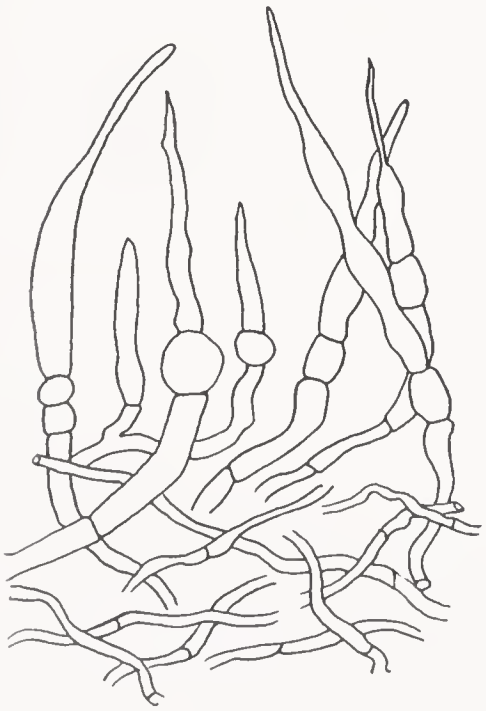
194 - mutabilis Murr.



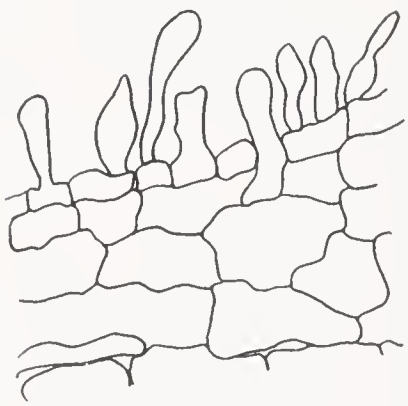
195 - crustosa Pk.



196 - chlorinosma Burl.

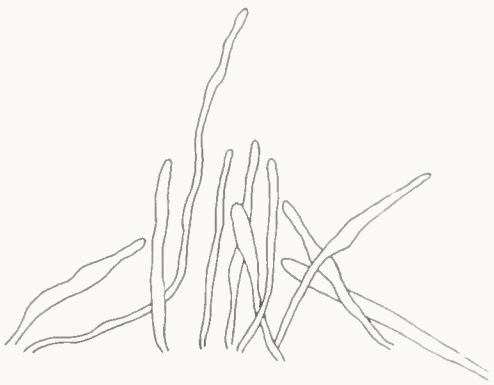


197 - mariae Pk.



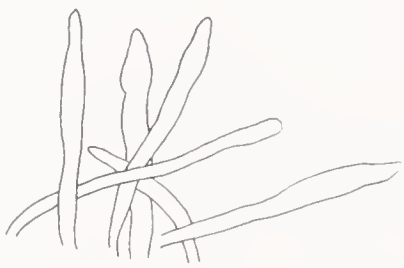
198 - albida Pk.

199 - hixsoni Murr.

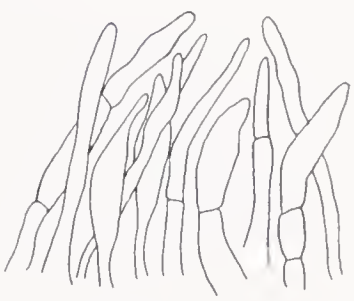


200 - albidicremea Murr.

201 - albiclavipes Murr.

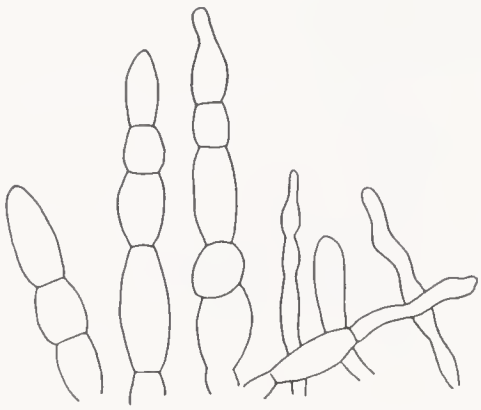


202 - glaucescentipes Murr.

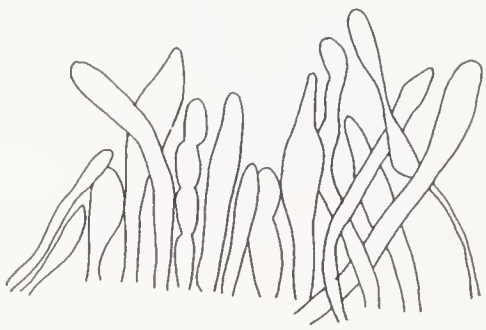


203 - subpruinosa Murr.

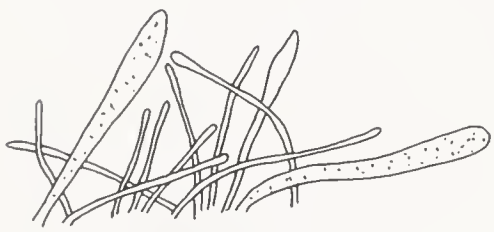
204 - rubripurpurea Murr.



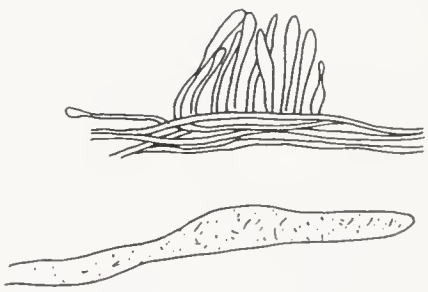
205 - tuberculata Murr.



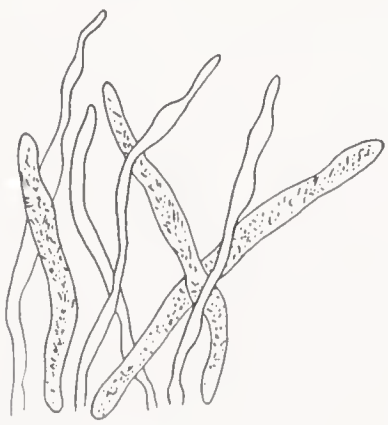
206 - praerubra Murr.



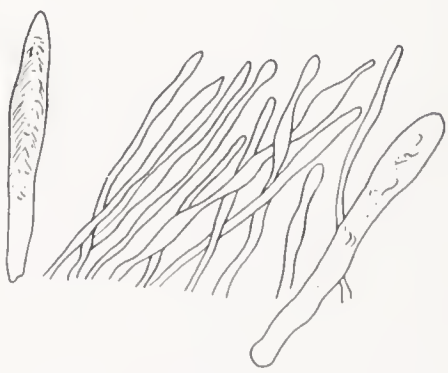
207 - peckii Sing.



208 - vesicatoria Burl.



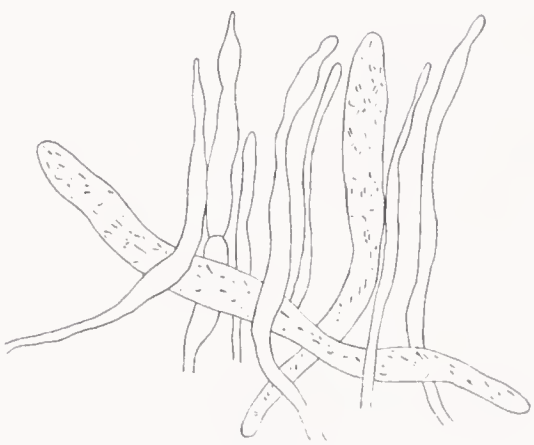
209 - emeticiformis Murr.



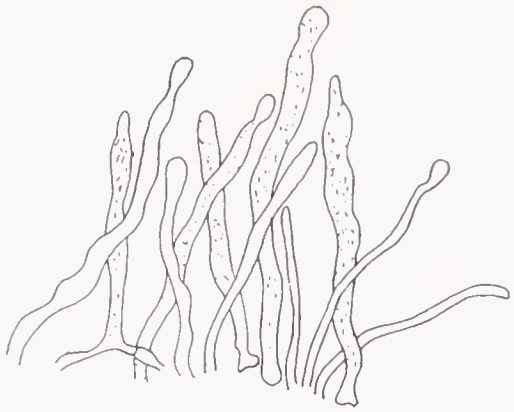
210 - macropoda Sing.

211 - variegata Sing.

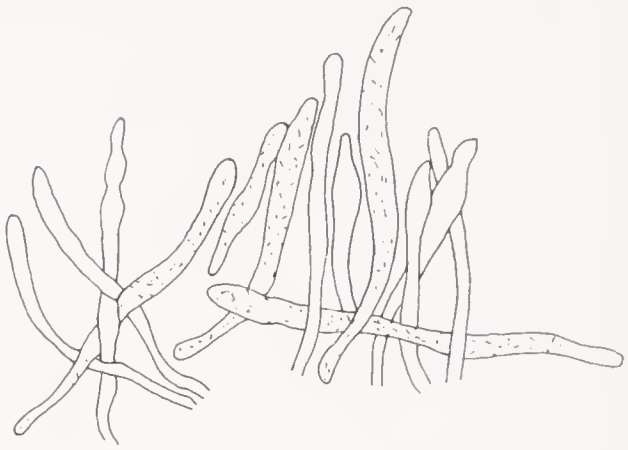
212 - serissima Pk.



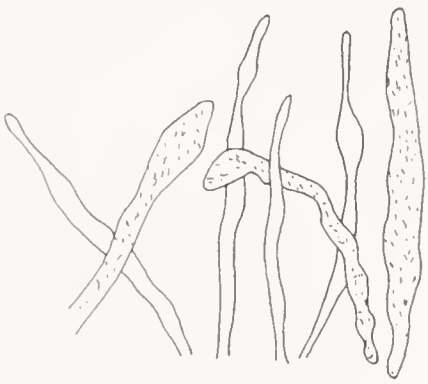
213 - vinacea Burl.



214 - furcatifolia Murr.

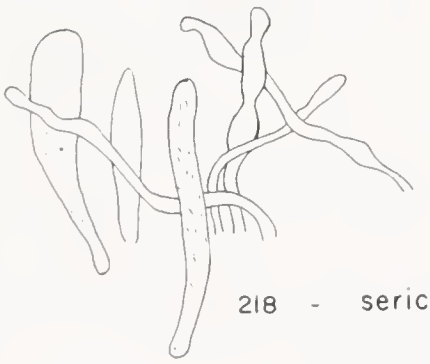


215 - subsericeonitens Murr.



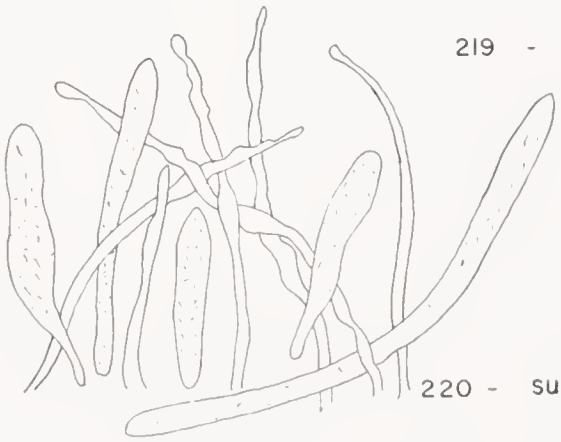
216 - uncialiformis Murr.

217 - rubrifolia Murr.



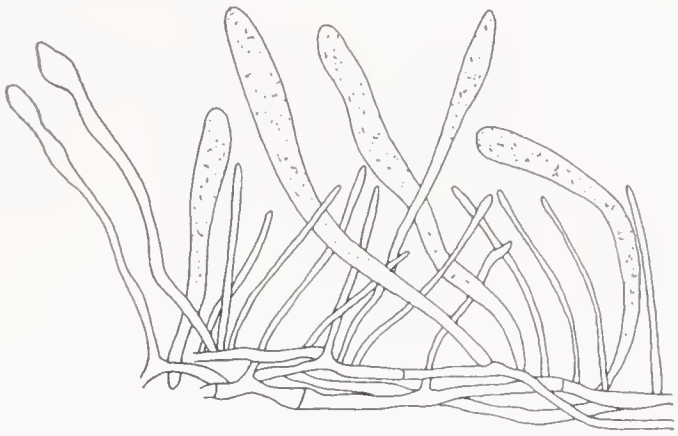
218 - sericella Murr.

219 - subpavonina Murr.



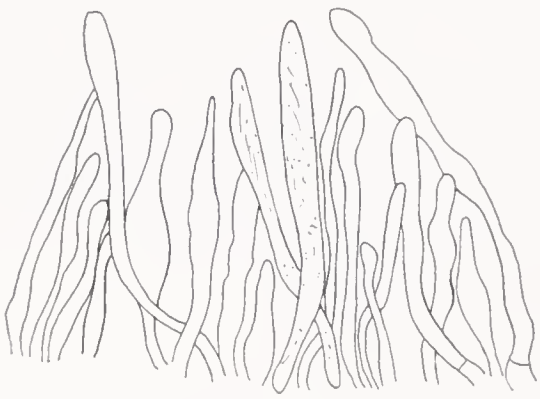
220 - subbrunneipes Murr.

221 - sericeonitens Kauff.

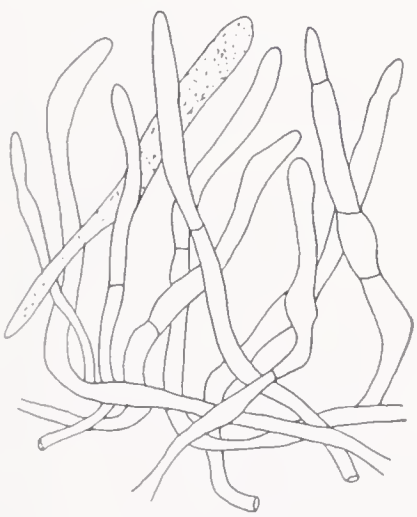


222 - simillima Pk.

223 - pungens Beards.



224 - magna Beards.



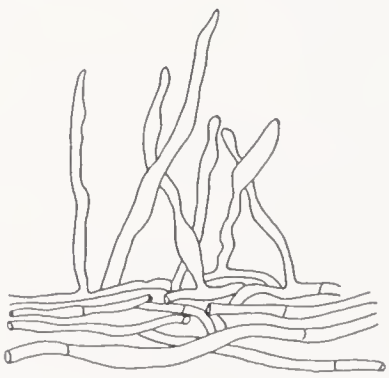
225 - pusilla Pk.

226 - tenuiceps Kauff.

227 - viridella Pk.

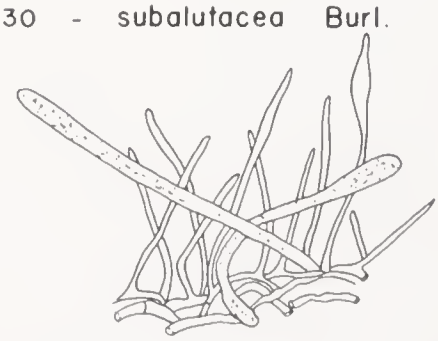
228 - nigrodisca Pk.

229 - rugulosa Pk.

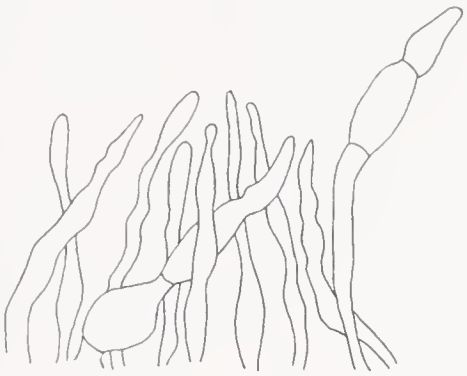


230 - subalutacea Burl.

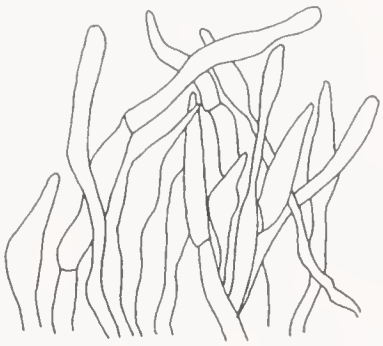
231 - subdepallens Pk.



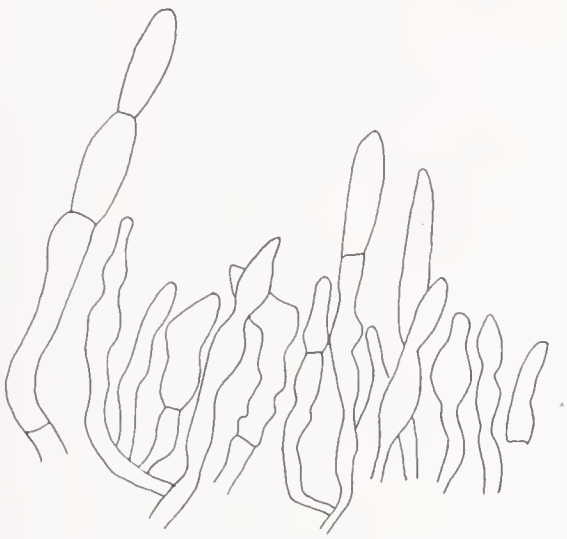
232 - palustris Pk.



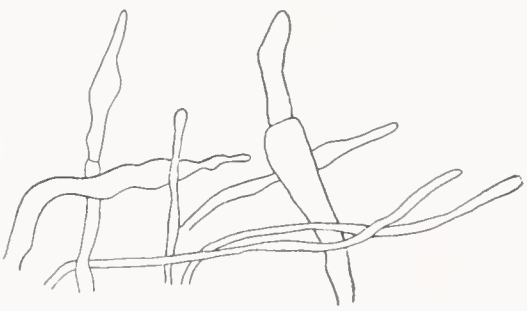
233 - crataegorum Murr.



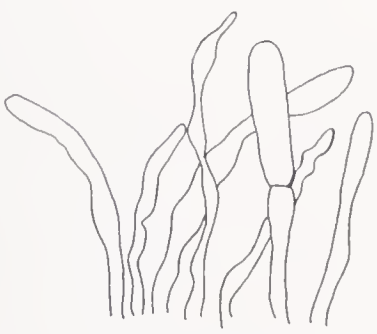
234 - borealis Kauff.



235 - amygdaloides Kauff.

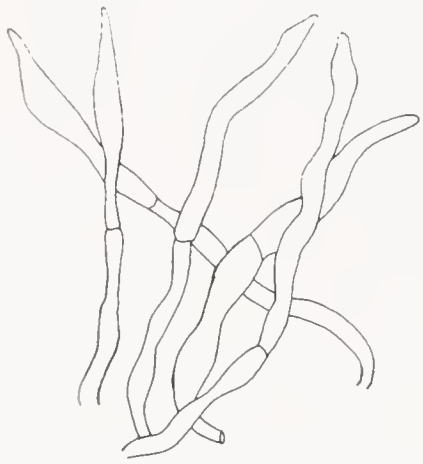


236 - cremeirubra Murr.

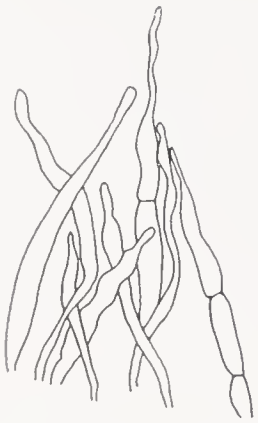


237 - cremeirosea Murr.

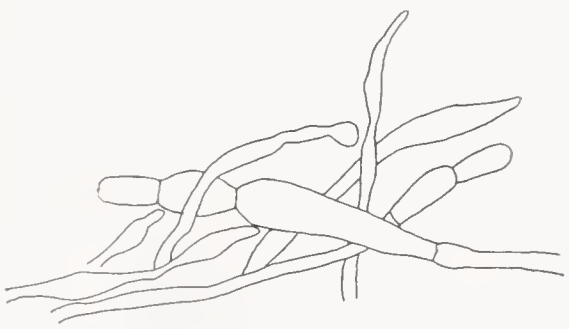
238 - ochrophylla Pk.



239 - corallina Burl.

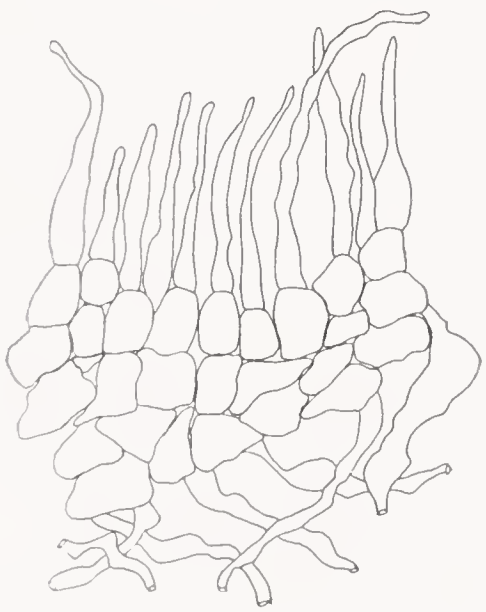


240 - glauca Burl.

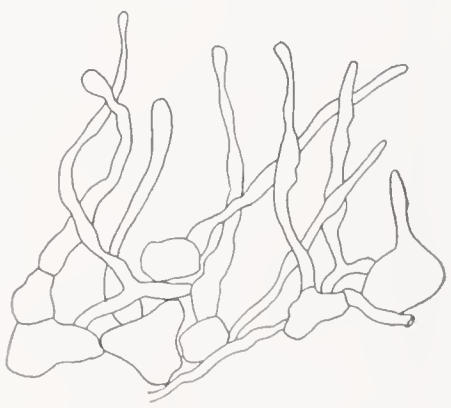


241 - roseitincta Murr.

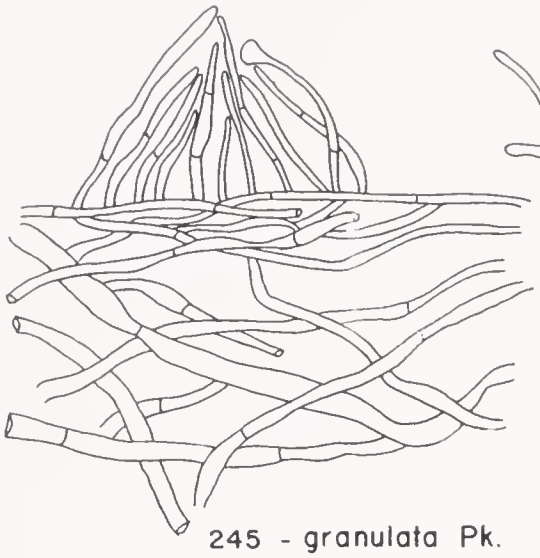
242 - mutantipes Murr.



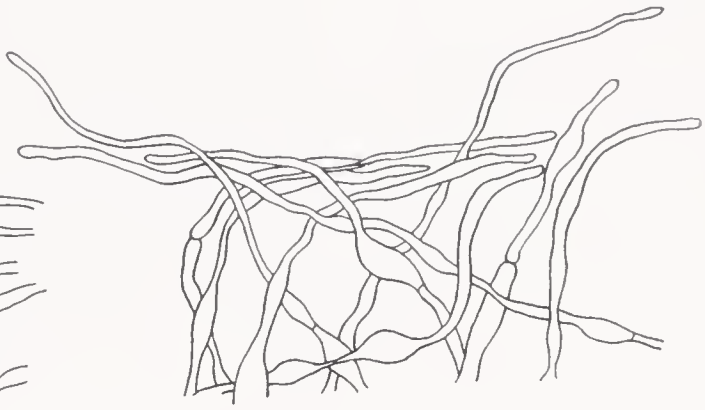
243 - rimosa Murr.



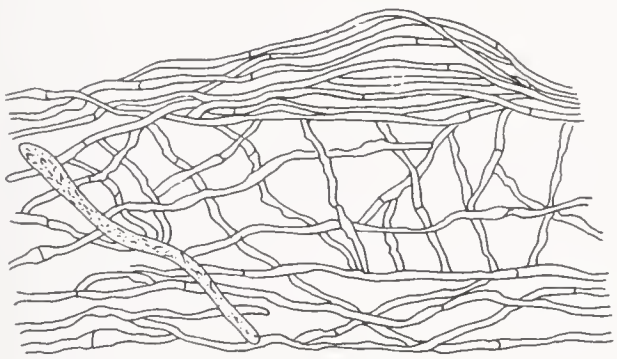
244 - praetenuis Murr.



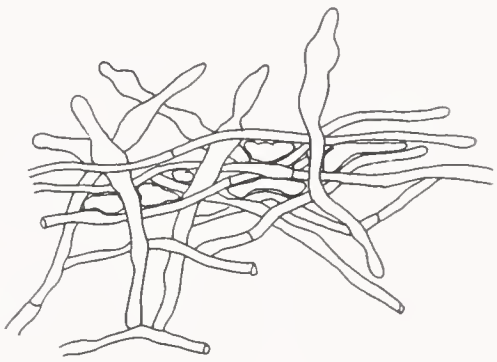
245 - granulata Pk.



246 - subsordida Pk.

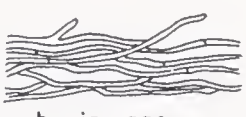


247 - balloui Pk.



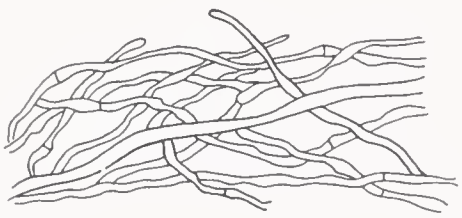
248 - pulchra Burl.

a. in youth

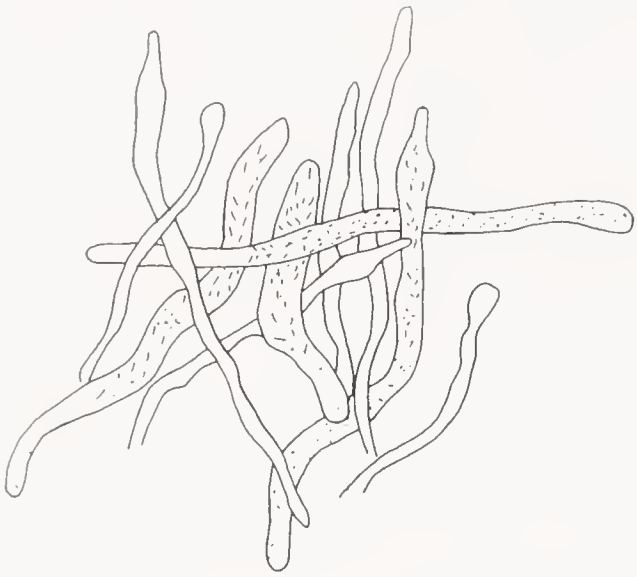


b. in age

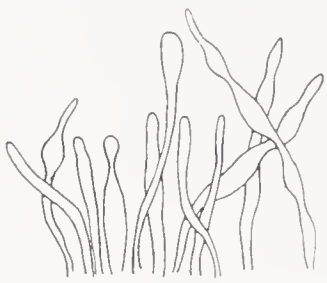
249 - magnifica Pk.



250 - pectinatoides Pk.



251 - anomala Pk.

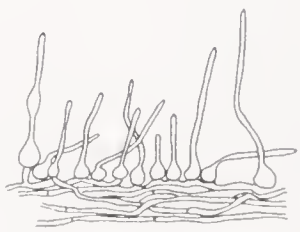


252 - albiduliformis Murr.

253 - brevipes Pk.

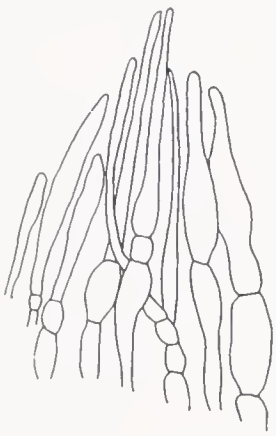
254 - pusilliformis Murr.

255 - atropurpurea Pk.

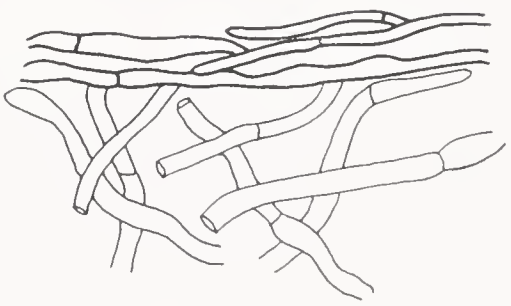


256 - nigrescentipes Pk.

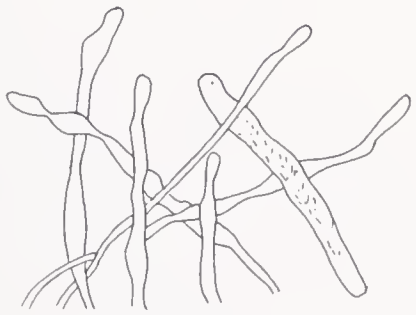
257 - granulosula Murr.



258 - lividirosea Murr.

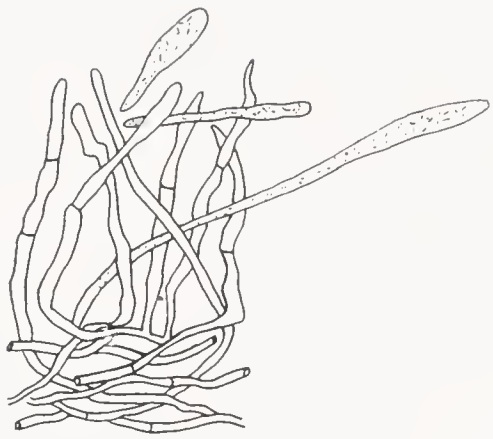


259 - compacta Frost & Pk.

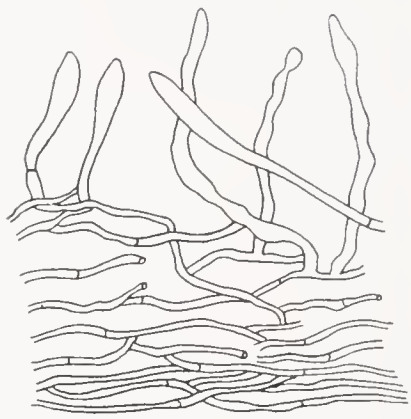


260 - obscuriformis Murr.

261 - subochrophylla Murr.

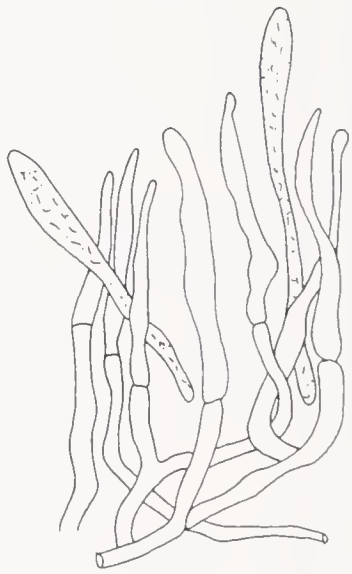


262 - blackfordae Pk.

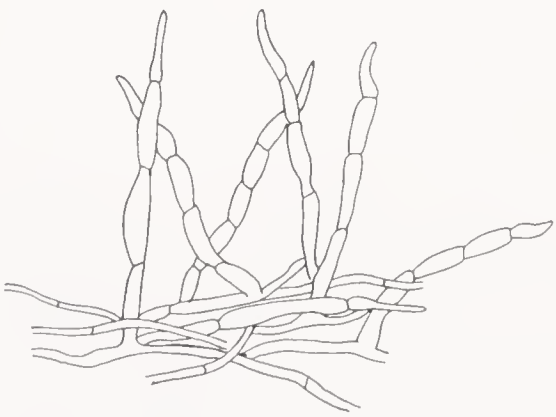


263 - flavida Frost & Pk.

264 - flaviceps Pk.

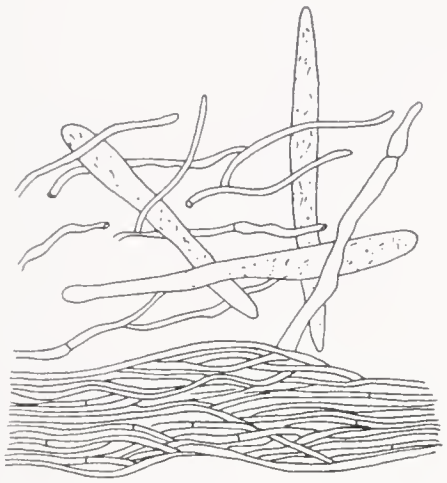


265 - cinerascens Beards.

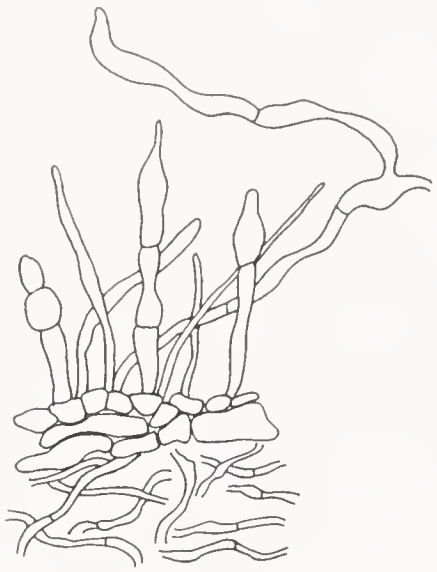


266 - earlei Pk.

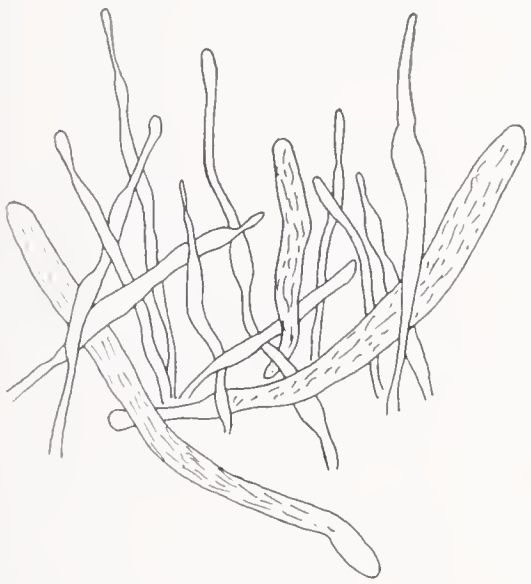
267 - pinicola Murr.



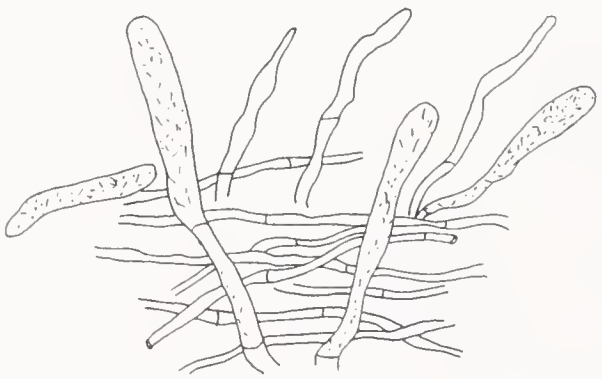
268 - perplexa Burl.



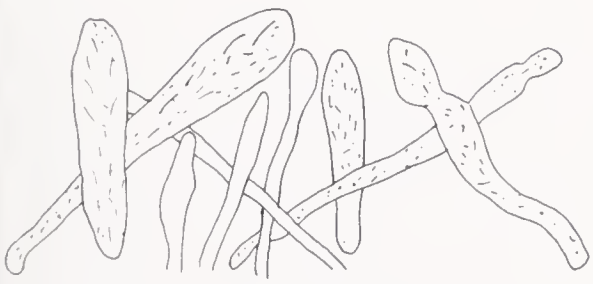
269 - uncialis Pk.



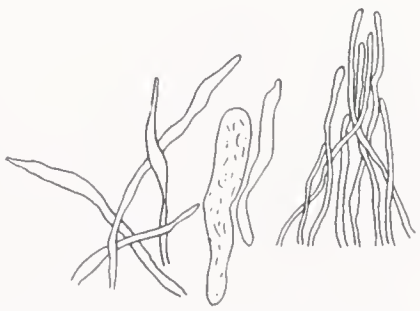
270 - burkei Burl.



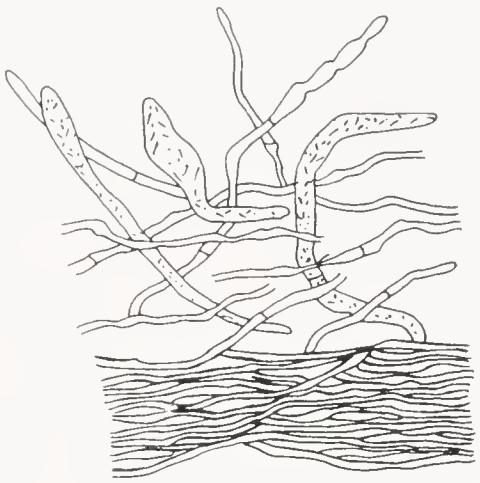
271 - admirabilis Beards. & Burl.



272 - perlactea Murr.

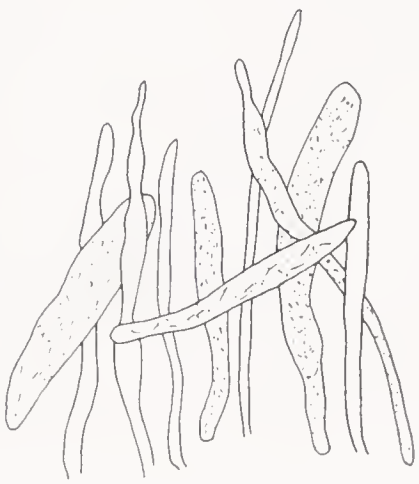


273 - praecompacta Murr.

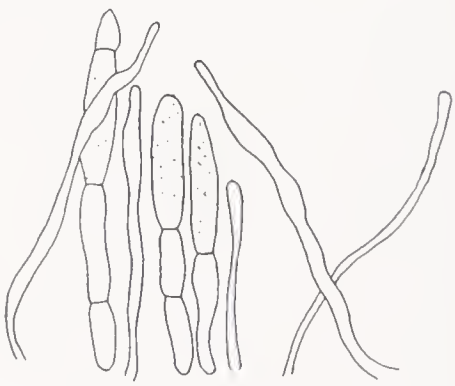


274 - albidula Pk.

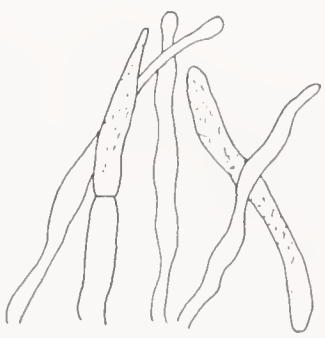
275 - leucomodesta Sing.



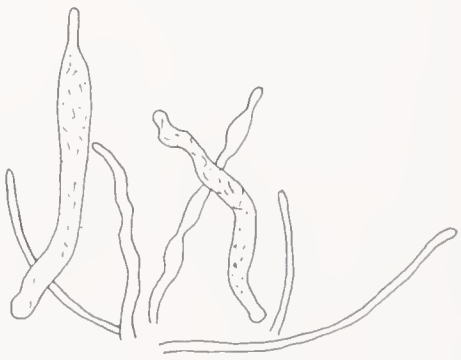
276 - inedulis Murr.



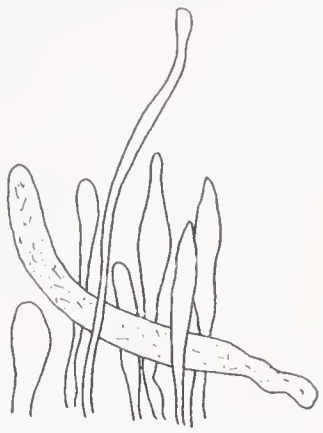
277 - luteispora Murr.



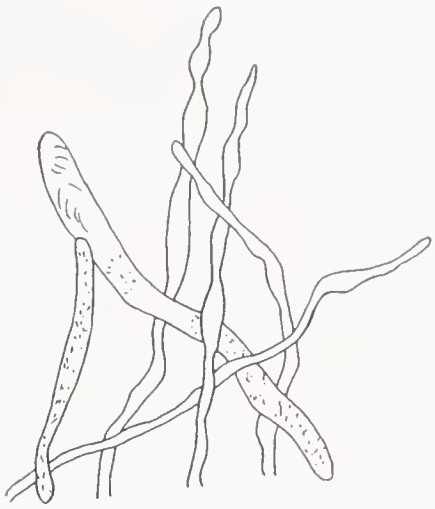
278 - incarnaticeps Murr.



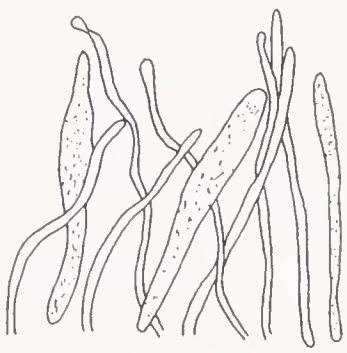
279 - fosteriana Murr.



280 - ferrotincta Sing.

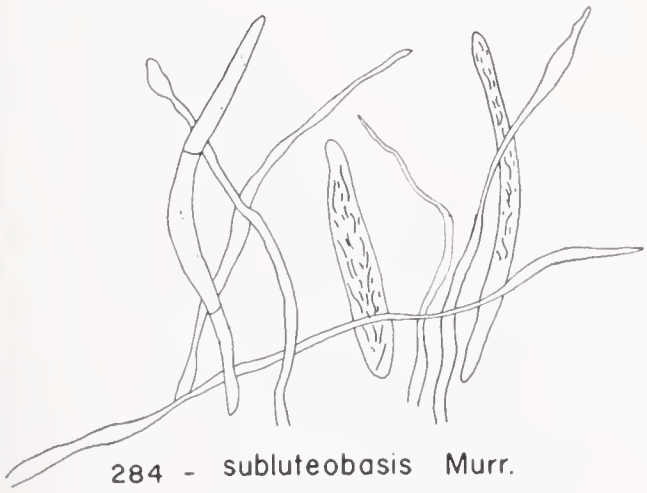


281 - cystidiosa Murr.

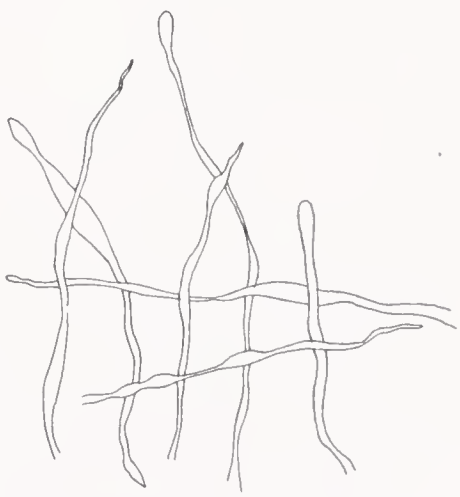


282 - aurantialutea Kauff.

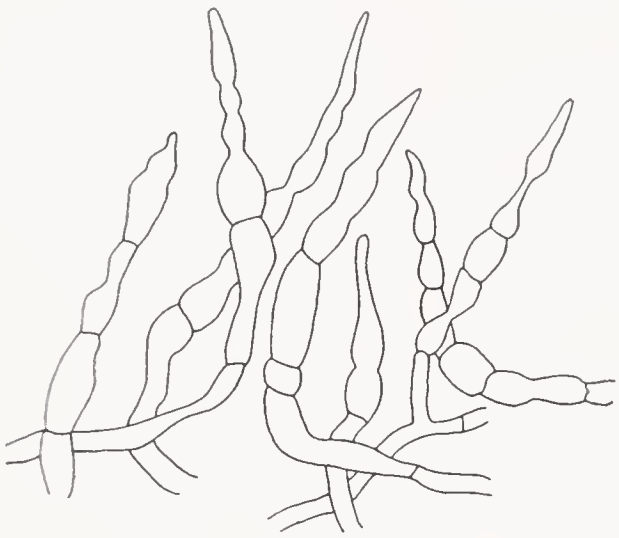
283 - diaboli Sing.



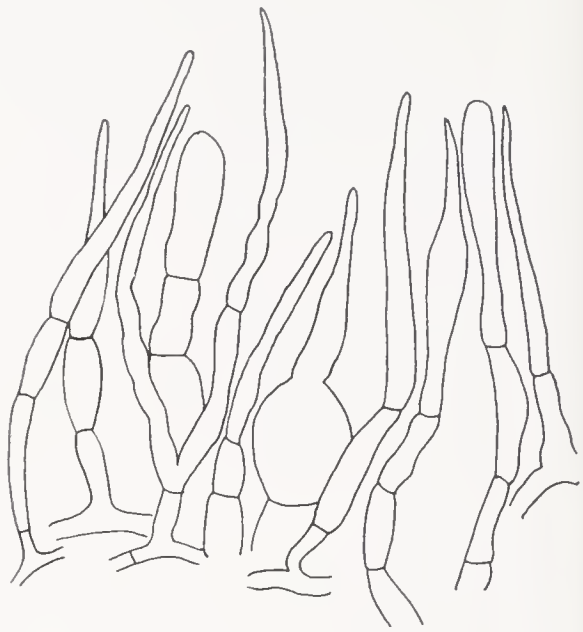
284 - subluteobasis Murr.



285 - cremea (Murr.) Sing.

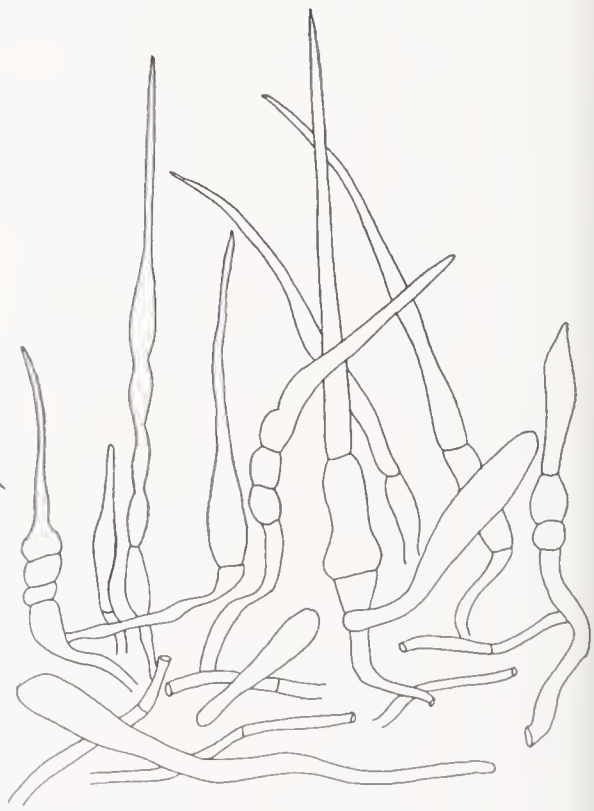


286 - brunneola Burl.

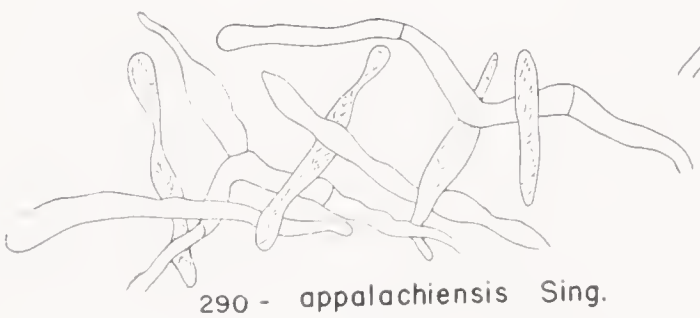


287 - variicolor Murr.

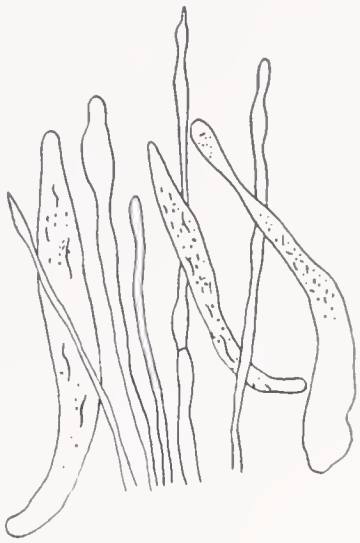
288 - flocculosa Burl.



289 - modesta Pk.



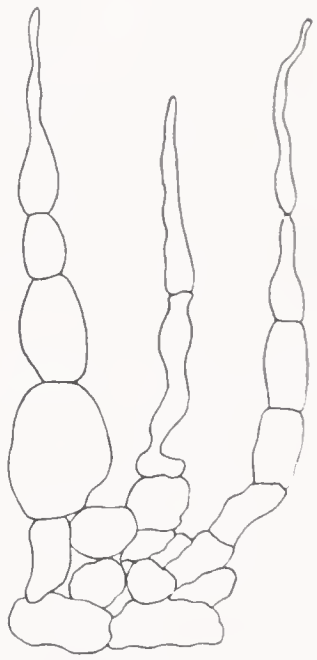
290 - appalachiensis Sing.



291 - pervirginea Murr.

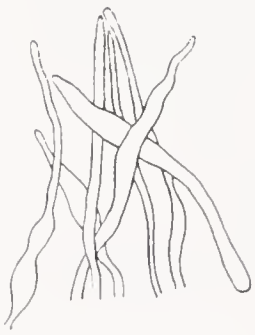
292 - beardslei Burl.

293 - patriotica Murr.

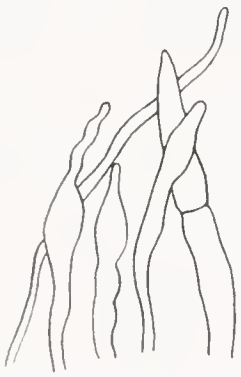


294 - maculosa Murr.

295 - albiflavescens Murr.

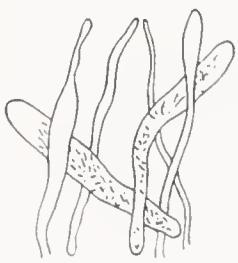


296 - arnoldae Murr.

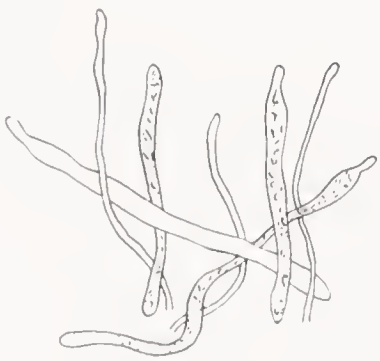


297 - australirosea Murr.

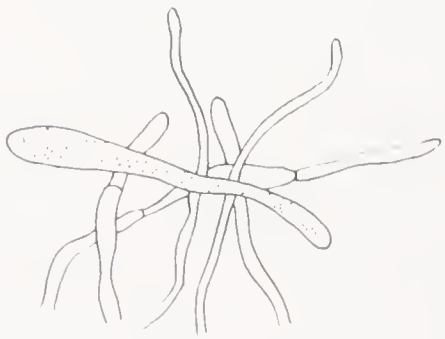
298 - variata Bann.



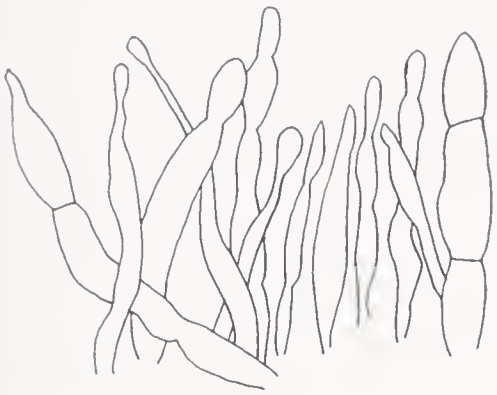
299 - alutaceiformis Murr.



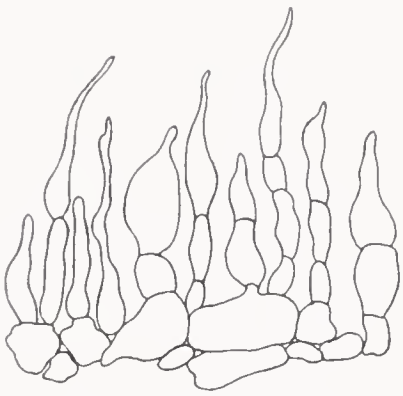
300 - albimarginata Murr.



301 - levyana Murr.

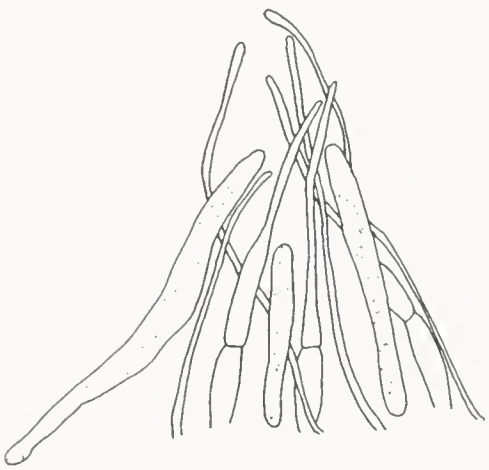


302 - subfloridana Murr.

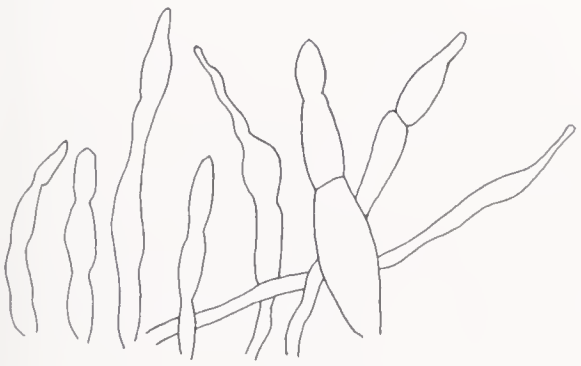


303 - subglauca Murr.

304 - novispora Murr.

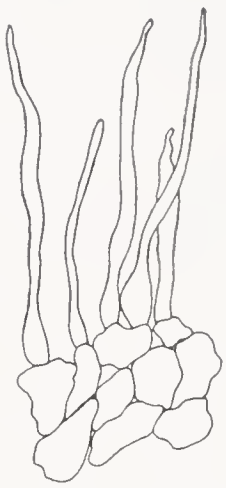


305 - xerampelina
var. semirubra Sing.

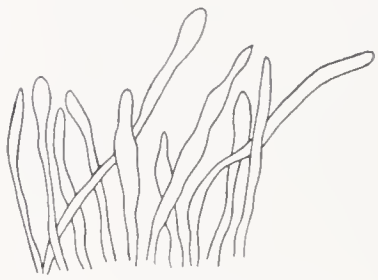


306 - regalis Murr.

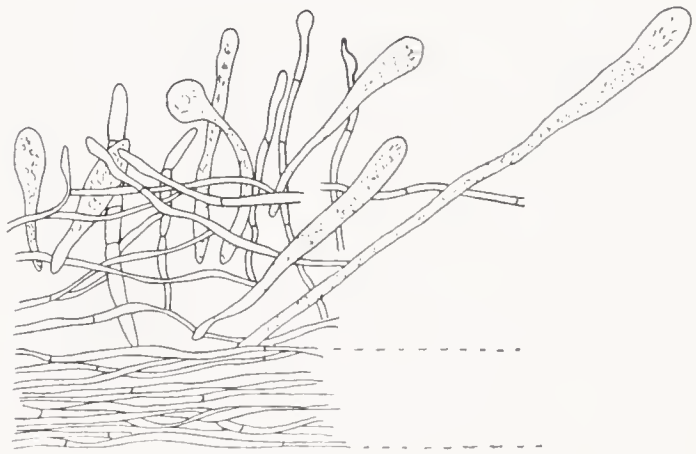
307 - pinetorum Murr.



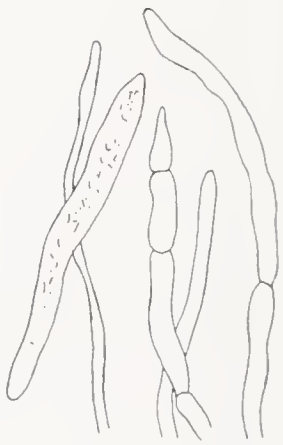
308 - rosei-isabellina Murr.



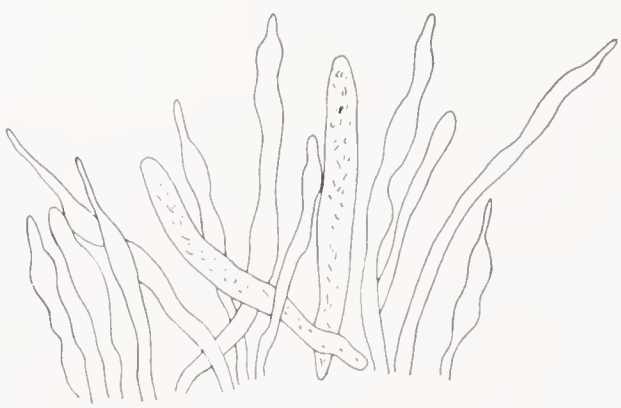
309 - pseudolepida Sing.



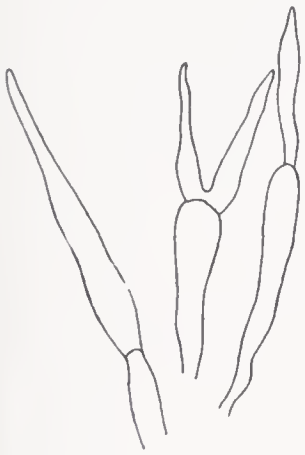
310 - subacris Murr.



311 - pinophila Murr.



312 - subcremeiceps Murr.



a. rare

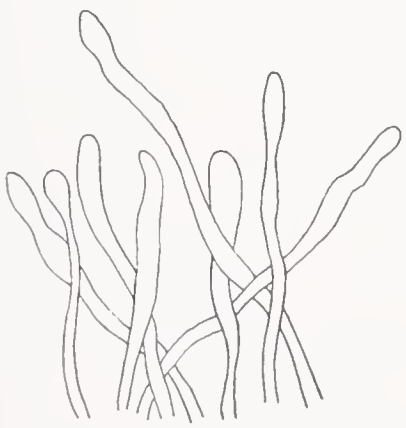
b. common

313 - subgraminicolor Murr.

314 - subsulphurea Murr.

315 - luteobasis Pk.

316 - vinosirosea Murr.



317 - subinconstans Murr.

318 - basifurcata Pk.

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BOTANICAL
GARDEN

Memoirs
of
The Torrey Botanical Club

Vol. 21, No. 3 December 1, 1960

Editor
MURRAY F. BUELL

STUDIES ON SECOTIACEOUS FUNGI IX THE ASTROGASTRACEOUS SERIES

By
ROLF SINGER AND ALEXANDER H. SMITH

Department of Botany, University of Tucumán
Tucumán, Argentina
AND
University of Michigan Herbarium and Department of Botany
University of Michigan, Ann Arbor, Michigan, U. S. A.

Published for the Club by
THE SEEMAN PRINTERY
Durham, N. C.

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teromyees. As a result of our different opinions on the trend of evolution, in our previous papers, (Singer & Smith 1958 a, b & c, 1959 a, b), we merely presented data on the genera and species involved. It was through Smith's persistence in the study of the species of *Arcangeliella* and *Hydnangium*, particularly in working over the collections in the herbarium of S. M. Zeller, which are now at the New York Botanical Garden, that the data to recharacterize many of the species and genera presented here was obtained.

The data he obtained from this study convinced him that it is impossible to logically defend the thesis that the Astrogastraceous Series is an evolutionary series leading from the agaric genera *Lactarius* and *Russula* to the Gastromycetes. Hence, in the discussion at the end of the presentation of our taxonomic data in the present paper, we have presented our opinions on the evolution of the Astrogastraceous Series.

Many of the specimens reported on in this paper were collected in the field by Smith during his expeditions to collect Agaricales in the western United States. For financial support in this work he wishes to acknowledge help from the National Science Foundation, the Faculty Research Fund of the University of Michigan, and the field expedition fund of the University of Michigan Herbarium. Also, funds from the National Science Foundation and the publication fund of the University of Michigan Herbarium have helped to defray the cost of publication.

Definition of the Astrogastraceous Series: As we define the genera which belong here they are characterized primarily by the context of the carpophore being composed of heteromerous tissue, and by the spores having typically an amyloid material covering all or part of the spore ornamentation. This definition holds until the *Hydnangium-Octavianina* level is reached. Here we begin to find examples in which the context of the gastrocarp contains only scattered sphaerocysts rather than the latter occurring in bunches, and the spore ornamentation is seen to become progressively less amyloid until species are encountered with inamyloid spore-ornamentation and scarcely any sphaerocysts in the tissues. At this level clamp connections finally occur, and similarities to other lines of agarics, such as *Laccaria* become apparent.

KEY TO THE GENERA OF THE ASTROGASTRACEOUS SERIES

1. Spore deposit not obtainable, the spores not forcibly discharged from the sterigmata — 2
1. Spore deposit readily obtained as in most Hymenomyeetes — 10
2. Sport ornamentation inamyloid — 3
2. Spore ornamentation amyloid at least in some part — 4
3. Clamp connections present; spore ornamentation in the form of warts and spines with free tips — *Hydnangium*
3. Clamp connections absent; latex present or absent — *Octavianina*

4. Stipe-columella absent as such, the sterile column reduced to a basal area of tissue with branches extending into the gleba from it (these may or may not reach the peridium); or no interior sterile structures present other than tramal plates 5
4. Stipe-columella well defined; gleba usually exposed at base of peridium (at the margin and on under side) and in age often separating from columella 7
5. Fresh specimens exuding a latex when cut . . . . . *Zelleromyces*
5. Latex absent 6
6. Mediostratum of tramal plates containing sphaerocysts *Gymnomyces*
6. Mediostratum of tramal plates lacking sphaerocysts *Martellia*
7. Latex present in fresh specimens . . . . . *Arcangeliella*
7. Latex absent 8
8. Mediostratum of tramal plates lacking sphaerocysts *Elasmomyces*
8. Mediostratum with at least scattered sphaerocysts 9
9. Cuticle of peridium of large pseudoparenchyma-like cells; leptocystidia typically present in hymenium . . . . . *Cystangium*
9. Cuticle of peridium various and hymenial cystidia mostly of the pseudocystidial and macrocystidial types (as in *Russula*) *Macowanites*
10. Latex present . . . . . *Lactarius*
10. Latex absent . . . . . *Russula*

HYDNANGIUM Wallroth

In Dietr. Flor. Boruss. [Flor. Königr. Preuss.] VII p. 465. 1839.

Gastrocarp globose to irregular, lacking a columella and or a sterile base; gleba chambered; latex absent; spores inamyloid; hyphae with clamp connections; sphaerocysts present or absent.

Type species. *Hydnangium carneum* Wallr.

This is to be regarded as the most primitive genus in the Astrogastraceous Series, because of the clamped hyphae and essentially non-amyloid spores. In checking the amyloid reaction on the spore ornamentation a lens of 1.3 N.A. was used, with, of course, the condenser immersed. The objective was a B. & L. appochromatic lens. With this system no amyloid reactions were visible on isolated spines in the mount, but only faintly on spines in place on the spores where it was difficult to exclude a slight shadow effect.

There has obviously been confusion in regard to species concepts and we are not in a position at present to even guess as to how many species may actually be hidden under the name *H. carneum*, but there have been more than one. All we can do now, as far as the genus is concerned is to present our studies as far as we have been able to carry them to date. As of this writing we believe we can recognize four species in the genus. The following redescriptions are based on a study of authentic material, as indicated, as far as such was available.

KEY TO SPECIES

1. Spores pseudo-amyloid 1. *H. nigricans*
1. Spores hyaline to yellowish in Melzer's reagent 2
2. Context of peridium showing scattered sphaerocysts 2. *H. soderstroemii*
2. Context of peridium lacking sphaerocysts 3
3. Oleiferous hyphae present 3. *H. roseum*
3. Oleiferous hyphae none 4. *H. carneum*

1. Hydnangium nigricans Kalchrenner, Grevillea 10:107. 1882.
Figs. 1-2.

Gastrocarps 15 × 20 mm, depressed-globose, smooth, black when dried; gleba ochraceous tawny, pale cinnamon as dried, cavities small and filled with spores; columella and sterile base lacking as far as known.

Spores 12-19 μ, globose, pale tawny to pale ochraceous in KOH (pigment fading somewhat on standing), rusty-brown (pseudo-amyloid) in Melzer's reagent; ornamentation in the form of broad cones about 1.5-2 × 1-2 μ; so closely arranged as to touch each other on all sides but not fused, their walls either not at all or only very inconspicuously striate; plage area not differentiated; sterigmal appendage seldom showing.

Hymenium. Very poorly revived in material available for study. "... Basidia 30 × 11 μ"—Dodge and Zeller (1936) p. 592.

Hyphal layers. Subhymenium gelatinous—disintegrating, hyaline; mediostratum apparently of broad (7-11 μ) interwoven hyphae which also disintegrate readily. Oleiferous hyphae 8-12 (15) μ broad present and staining brightly in phloxine. Epicutis of peridium of rusty brown thin-walled hyphae more or less interwoven and progressively with less pigment interiorly, the cut ends giving a cellular appearance. Context of interwoven hyaline hyphae and oleiferous hyphae. *Clamp connections present.*

Under Acacia, grassy area, near Somerset, East C.R.S. Feb. 1876. leg. Macowan (type) (Zeller Herb., NY).

In the portion of the type in the Zeller collections at New York only the oleiferous hyphae, the presence of clamps, and the spores could be critically studied. The spores are paler in color than those of *Octavianina nigrescens* but of the same tone and in addition are pseudoamyloid. *H. nigricans* appears to be a species closely related to *O. nigrescens* but differs in the presence of clamp connections.

2. Hydnangium soderstroemii Lagerheim in Patouillard et Lagerheim, Bull. Soc. Myc. France 9:142. 1893.
Fig. 3.

Gastrocarp 3-4 cm broad; globose to subglobose, strongly gibbous, rounded above, flattened below, base attenuate, short; peridium thin, evanescent, flesh-reddish; gleba pallid whitish-incarnate; chambers sinuous, small 0.25 mm long, empty, tramal plates somewhat thickened, radiating from the base. Basidia 70 × 8-10 μ, 2-spored, subcylindric, cystidia none; spores globose, 12-15 μ in diam., echinate, warts obtuse, short, thickish.

A portion of the type in the Zeller Herbarium was studied and the following data are here reported.

Spores 10-15 μ in diam., globose, wall 1.5-2 μ thick, ornamentation about 2 μ high in the form of cones 2 μ broad at base, wall and cones not amyloid (possibly with a slight amyloid reaction around the base of the spines); elements of ornamentation readily deciduous; sterigmal appendage conspicuous as a broken filament with undulating walls.

Hymenium. Basidia 1-, 3-, but mostly 2-spored, 45-66 × 9-11 μ without sterigmata, mostly remaining partly collapsed but sterigmata clearly evident. Cystidia absent or if present resembling 1-spored basidia, rare.

Hyphal layers. Tramal plates of interwoven hyphae, some sphaerocysts observed in slightly crushed sections; subhymenium remaining indistinct (apparently of compactly interwoven hyphae). Epicutis of peridium of interwoven appressed hyphae. Context of interwoven hyphae and some sphaerocysts. Clamp connections present.

A study of the type of *Octaviania stillingeri* Lloyd gave data identical to that of the type of *H. soderstroemii* except for the shorter basidia (30-40 × 9-11 μ). We believe that *H. stillingeri* is properly placed in synonymy with *H. soderstroemii* as has been proposed by other authors. The difference in the length of the basidia might possibly be significant, but this would have to be established by studies of ample specimens in the fresh state. The pale incarnate tint to the gleba indicates a close relationship to *H. carneum*, but the presence of sphaerocysts in the context of the peridium indicates a slight progression toward the more clearly defined portion of the Astrogastraceous Series.

We are recognizing *H. soderstroemii* as a distinct species from *H. carneum* because of confusion as to the true concept of *H. carneum* and the fact that we have actually studied the type of *H. soderstroemii* and demonstrated the important characters as these are given in this work. If indeed the true *H. carneum* does have sphaerocysts in the peridium, the question of whether *H. soderstroemii* is a synonym will have to be reviewed again, but as of this writing we would assign all the collections as indicated in our key. Hesse's account of the anatomy of the peridium of *H. carneum* did not indicate the presence of sphaerocysts, which, again, is in line with the data taken from Murrill's collection of the latter.

3. Hydnangium **roseum** (Harkness) Singer & Smith comb. nov.

Octaviania rosea, Harkness, Bull. Cal. Acad. Sci. 1:29. 1884.
Arcangeliella rosea (Hark.) Zeller & Dodge, in Dodge, Ann. Mo. Bot. Gard. 18:462. 1931.

Fig. 4.

"Gregarious, peridium fibrillo-rugose, irregularly lobed, 1-3 cm in diam., with distinct absorbing base, pale rose color, deepening within; basidia 1-, 2-spored; sterigmata filiform, capitate, as long as the diameter of the spore; spores globose, hyaline, pale, epispore covered with short, obtuse spines, 14-17 μ."

"Under shrubby oaks, at Golden Gate Park, San Francisco, Calif. January" (quoted from Harkness, p. 252, 1899).

The specimen studied was collected by Harkness at San Francisco and distributed as No. 3238 in Rabenhorst-Winter, Fungi Europei. The following data were obtained from it:

Spores globose, 10-15 μ; sterigmal appendage a short or long (depending on where the sterigma breaks) filament, with parallel walls that are thin, hyaline and non-amyloid; spore wall 1.5(2) μ thick, inamyloid (yellow in Melzer's reagent), ornamentation essentially inamyloid, consisting of pointed cones 1.3-1.8(2) × 1.3-2 μ, cones separate but closely spaced, after standing in Melzer's reagent for about a half hour a slight darker spot, almost shadow-like could be seen on some cones near apex, (so there is a possibility of a very slight amyloid reaction there).

Hymenium. Basidia 26-24 × 10-13 μ, almost oval when young, 2-spored (rarely 1-spored), readily collapsing; sterigmata conic before spore forms, then the wall parallel in upper part and base enlarged, 9-12 μ long overall and 2-3 μ wide at base. Basidioles 18-20 × 10 μ, basidia project strongly above them when sporulating. Cystidia none unless some 1-spored basidia actually remain sterile.

Hyphal layers. Tramal plates of interwoven filaments 4-11 μ diam. and with hyaline walls; no sphaerocysts found (sections revived very well); subhymenium appearing cellular from broad ends of cut hyphae—about the diameter of the base of the young basidium; no true sphaerocysts seen in the layer. Epicutis of peridium of appressed-interwoven, hyaline, hyphae not sharply differentiated from the filamentous context; clamp connections present; no sphaerocysts or laticiferous hyphae seen; oleiferous hyphae present.

We here maintain Harkness's species as distinct from *Hydnangium soderstroemii* because of the lack of sphaerocysts in the peridium and tramal plates, and the shorter broader basidia. There is no question but that the two species are very closely related, but lacking critical studies of fresh gastrocarps, we cannot be sure at present that there are not other differences, not now apparent. It is clear from the material in the Zeller Herbarium (NY) that more than one species was included under the name *Arcangeliella rosea*.

4. Hydnangium carneum Wallr. in Dietr. Flor. Boruss. [Fl. Königr. Preuss.] VII p. 465. 1839.

Fig. 5.

Gastrocarp 10-25 mm broad, occasionally larger (± 35 mm), globose to depressed or variously irregular, dull reddish when young, later shining and flesh-color; with a rather strong basal attachment of mycelium, rhizomorphs not present. Gleba at first fragile becoming fleshy; dull reddish young, later flesh-colored, chambers rather spacious and, especially in the center, quite irregular in form; columella none, sterile base present as a mycelial tissue-like pad at point of attachment.

Spores 11-15 μ diam., globose, hyaline in KOH, pale yellow in Melzer's reagent and ornamentation inamyloid; ornamentation in the form of pointed cones 1.7-2.2 μ high and 1-1.7 μ at base, separate but often touching at their bases; spore wall 0.8-1.3 μ thick; sterigmal appendage short and inconspicuous; plage area not different from remainder of surface.

Hymenium. Basidia 2-spored, 40-52(65) × 10-13 μ, narrowly clavate to subcylindric, thin-walled, readily collapsing, basidioles also readily collapsing. Cystidia none. Pseudoparaphyses none.

Hyphal layers. Subhymenium of hyphae 5-10 μ broad, compactly arranged but thin-walled and delicate, collapsing readily, giving a cellular appearance in sections but basic arrangement not clear from dried material; mediostratum of interwoven hyaline smooth, thin-walled hyphae 6-12 μ diam., the cells somewhat inflated and readily collapsing, no sphaerocysts seen. Epicutis of pileus of thin-walled hyaline hyphae 3-8 μ diam. and readily collapsing, the zone not distinctly separated from context. Context of interwoven hyaline hyphae 5-12 μ diam., very delicate and readily

collapsing; sphaerocysts none; oleiferous hyphae none. Clamp connections present.

Jamaica, Dec. 25, Jan. 8, 1908-09, W. A. Murrill. (NY).

The above is a composite description of macroscopic characters taken from Hesse's account of the species in Europe and microscopic data taken from Murrill's collection. This was done because all the available data on microscopic characters as given by Hesse also checked with those of the Murrill collection—in other words, as near as we can tell, the latter is correctly identified. Murrill's material was abundant, well dried and is in a good state of preservation at present. No. 109, *Octaviania carnea*, of de Thümen, Mycoltheca universalis, leg. L. Becker, Breslau, 1873 has spores exactly as in Murrill's collection but there was not enough peridium present for a critical study. Hence we used Murrill's collection.

We suspect that this species is not referable to the Astrogastraceous Series, or if so, it is at a level where several lines traceable up to the agarics diverge. On the sum total of all its characters including the color of the tramal plates when fresh, the hyaline non-amyloid, strongly echinate spores, long basidia and broad hyphae of the mediostratum of the tramal plates, this species resembles what one would expect to find in a gastroid *Laccaria* and a true relationship, in our estimation, is highly probable.

H. roseum is not really very distinct from *H. carneum*, but for the time being we recognize both on the presence or absence of oleiferous (or laticiferous?) hyphae, the character which Zeller and Dodge used to place *H. roseum* in *Arcangeliella*.

OCTAVIANINA O. Kuntze

Rev. Gen. Pl. 3^2:501. 1898.

Gastrocarp globose to irregular, usually less than 5 cm broad; peridium typically unpolished, thin, tissue with or without sphaerocysts, epicutis not clearly defined; gleba chambered; columella reduced to a sterile base or none; spores non-amyloid or essentially so, usually pseudo-amyloid, ornamentation typically coarse; clamp connections absent; latex present or absent.

Type species. *Octavianina asterosperma* (Vitt.) O. Kuntze.

We are inclined to agree with Zeller and Dodge (1936) that since Vittadini indicated that *Octaviania asterosperma* is aberrant in his genus *Octaviania*, it is undesirable to regard it as the type species for that genus. Following the proposal of Zeller and Dodge to consider *O. variegata* Vitt. as the type of *Octaviania*, and this appears to be the most logical procedure, the name *Octaviania* goes into synonymy under *Melanogaster*. By selecting *Octavianina asterosperma* as the type of Kuntze's genus, the latter becomes meaningful as a genus near the gastromycete end of the Astrogastraceous Series.

It is in this group of species that we believe the two lines, one leading to *Russula* and the other to *Lactarius*, diverge. It is significant that at this stage the spores for all practical purposes are inamyloid but that sphaerocysts are present in the mediostratum of the tramal plates and in the peridium of some species. Thus *Hydnangium* is to be regarded as

even more primitive, since, in addition to the reduction in sphaerocysts, clamp connections are present.

In this group of species, based largely on the coarse ornamentation of the spores, their pseudoamyloid reaction, and the absence of clamp connections on the hyphae of the gastrocarp, we note the primitive nature of the heteromerous tissue—sphaerocysts present in the peridial context in *some* of the species but these elements not in nests or groups—and the first demonstratable signs of the presence of amylaceous material on the spore ornamentation. Also the spore color in KOH is generally darker than found in the Russulaceae—usually cinnamon buff to pale tawny. A feature we believe is very important from the standpoint of evolution. A further feature of the spores of a number of the species is the presence of longitudinal striations on the elements of the ornamentation. In *O. nigrescens* the warts are of a primitive (relatively generalized) type with conspicuous striations whereas in species with more perfectly formed warts and spines, the striations are less conspicuous.

A second interesting feature is the number of species which show significant color changes when bruised. Agaric specialists have, of course, long been cognizant of the importance of these color changes in the recognition of species, but in the gastromycete literature such changes have not had the attention they deserve. This, again, re-emphasizes the need to study critically hypogeous gastromycetes in the fresh condition just as is now generally done with species of the Agaricales.

The absence of clamp connections on the hyphae of the gastrocarp is the deciding character separating *Octavianina* from *Hydnangium*. Thus *H. nigricans* appears to be a borderline species, since it has the pseudoamyloid spores of *Octavianina*, but is placed in *Hydnangium* because of the clamp connections. It is also interesting to note that in this group, where the diagnostic characters of the Russulaceae are found in a primitive, generalized state, that the peridium shows consistently a relatively undifferentiated type of structure, namely the lack of a specialized epicutis.

KEY TO SPECIES.

1. Spores 17-23 × 12-15 μ, ornamentation as spines 1-1.5 × 0.5 μ, yellowish in Melzer's reagent . . . . . 5. *O. macrospora*
1. Spores smaller and globose to subglobose 2
2. Spore ornamentation in the form of both ridges and warts . . . . . 6. *O. flava*
2. Spore ornamentation as distinct warts and spines 3
3. Gastrocarps white when fresh, soon blackening where handled or bruised 4
3. Gastrocarps not blackening as above 5
4. Context of peridium containing sphaerocysts . . . . . 7. *O. asterosperma* var. *potteri*
4. Context of peridium entirely of filamentose hyphae . . . . . 8. *O. nigrescens*
5. Cystidia present in the hymenium 6
5. Cystidia absent from hymenium 7
6. Latex absent . . . . . 9. *O. rogersii*
6. Latex present . . . . . 10. *O. papyracea*
7. Gastrocarp warty to uneven, white, becoming yellow where handled . . . . . 11. *O. tuberculata*
7. Not as above 8
8. Pseudoparaphyses with thickened walls; gastrocarp white, becoming red when injured . . . . . 12. *O. lutea*

8. Not as above 9
9. Surface of gastrocarp loosely fibrillose and yellowish white; peridium breaking up into small patches ..... 13. *O. lanigera*
9. Gastrocarp smooth and silky, continuous, whitish but slowly becoming brownish ..... 14. *O. laevis*

5. Octavianina **macrospora** Singer & Smith sp. nov.
Fig. 6

Carpophoris circa 1 cm latis, subalbis, glabris; gleba pallida, locellis minutis irregularibusque; sporis 17-23 × 12-16 μ, ellipsosoideis, suboehraceis, inamyloideis, echinatis. Specimen typicum legit prope "Twin Bridges Forest Camp" Clackamas Co., Oregon. August 9, 1937, D. P. Rogers (NY).

Gastrocarp about 1 cm diam. white when fresh, gray as preserved in liquid, glabrous; gleba of open chambers, presumably white when fresh; sterile base present and concolor with gleba as preserved.

Spores 17-23 × 12-16 μ, broadly ellipsoid, inner wall 1.5-2 μ thick; pale buff in KOH and pale ochraceous in Melzer's reagent; sterigmal appendage sometimes conspicuous, often slightly irregular in outline, hyaline-yellowish in Melzer's sol.; ornamentation in the form of short spines 1-1.5 (2.5) × 0.5 μ entirely non-amyloid (pale yellowish throughout in Melzer's solution), the elements distinct but often touching at their bases.

Hymenium. Basidia 1-, and 2-spored, 29-37 × 10-13 μ, clavate, thin-walled, content granular and ochraceous in KOH. Basidioles numerous. Cystidia none.

Hyphal layers. Subhymenium appearing cellular in section from the cut ends of hyphal branches, hyphae about the diameter of the base of the basidium, 1-2 cells below the cross wall cutting off the basidium the cells enlarging in age to sphaerocyst proportions; mediostratum filamentous, the cells of the filaments scarcely enlarged, walls thin and hyaline, no sphaerocysts present. Epicutis of peridium a collapsed turf of clavate to cystidioid cells 18-27 × 4-8 μ or 20-30 × 3-5 μ if fusoid. Context of hyaline interwoven subgelatinous (in KOH) hyphae 3-6 μ diam., no sphaerocysts or oleiferous hyphae in the layer. Clamp connections none.

Under hemlock, Twin Bridges Forest Camp, Clackamas County, Oregon, August 9, 1937. Coll. D. P. Rogers. Identified questionably as *Hydnangium album* by Zeller (Zeller Herb., NY).

The spores remind one of those of *Martellia ellipsospora* but have thicker walls and are completely inamyloid. The turf of cystidioid elements as the epicutis of the gastrocarp of *O. macrospora* is a further important distinguishing character.

6. Octavianina **flava** (Rodway) Singer & Smith comb. nov.
Gymnomyces flavus Rodway, Papers & Proc. Royal Soc. Tasmania 1917:110. 1918.
Fig. 14.

Gastrocarps 1-2 cm diam., drying dull buff (near "pinkish buff"), surface unpolished (as dried) and with bits of imbedded debris, surface showing the outline of the glebal chambers—hence peridium very thin; gleba chambered, chambers irregular in shape and *almost* filled, near

cinnamon buff in color, no columella or veins visible in the specimen studied.

Spores 9-12(14) μ (less ornamentation), yellowish-hyaline in KOH, pale orange-brown in Melzer's reagent (*not* dark brown), ornamentation in the form of short, broad, ridges and crests often irregular in outline and with some isolated warts, height of large warts 1-2.3 μ high, 1-2 μ broad at base, ridges about 1 μ thick and 5-10 μ long, typically inamyloid but some shadow-like local areas seen along the crest of some ridges or near the apex of some warts (usually only on one side); sterigmal appendage inconspicuous.

Hymenium. Basidia 26-33 × 10-15 μ clavate, none seen with sterigmata, thin-walled, readily collapsing. Cystidia rare, clavate to narrowly fusoid ventricose, 34-48 × 7-12 μ, content homogeneous or with some refractive material.

Hyphal layers. Subhymenium of filaments 7-10 μ broad, many-septate (hence subhymenium appearing cellular in section). Mediostratum of heteromerous tissue, mostly of large sphaerocysts. Peridium of heteromerous tissue; epicutis not clearly revived but apparently filamentous; laticiferous hyphae none. Clamp connections none found after careful observation.

Material studied. Rodway No. 1276, Wedge Bay, Tasmania, and No. 090 (Lloyd colls.) by L. Rodway, Hobart, Tasmania. Both from the Zeller Collections (NY).

We regard this at present as a valid *Octavianina* because of the clearly heteromerous tissue and essentially non-amyloid spore ornamentation. As far as could be ascertained the epicuticular zone is not cellular. The specimen used in our study could by no means be construed as young, except for its size. All the elements of the sterile tissues were completely expanded, and the collapsed basidia and abundant spores are additional evidence for judging the specimen as past maturity.

Our macroscopic data are taken from the specimen studied, except for size, because there is always the chance that the type collection contained several species. There is no doubt in our minds as to the desirability of removing this species from *Arcangeliella*, and we feel confident it is not synonymous with *Arcangeliella tasmanica*. If the type of the latter is actually lost the name should be discarded.

We place this species along side of *O. asterosperma* because of basic similarities in the spore ornamentation and structure of the peridium.

7. Octavianina asterosperma (Vitt.) O. Kuntze, Rev. Gen. Pl. 3²:501. 1898. var. *potteri* Singer & Smith var. nov.

Fig. 9.

Sporis inamyloideis; latice nullis. Specimen typicum legit prope Ithaca, Mich. Sept. 17, 1949, V. Potter *8898* (MICH.).

Gastrocarp 1-3.5 cm diam., roughly ellipsoid to globular in shape, surface glabrous, unpolished and dull grayish brown in darker areas, paler to pallid elsewhere as dried, white when fresh, blackening when handled; gleba watery white, drying rusty brown, chambers somewhat radially arranged; columella present as a pulvinate sterile base; attached by a small padlike stem.

Spores 12-16(18) μ in diam., including ornamentation, ornamented with large conic to blunt warts 2.5-3.5 × 2-3 μ, their walls yellowish in KOH and tawny to red-brown in Melzer's reagent, no distinct amyloid spot or area anywhere; sterigmal appendage a filament 4-8 μ long, 3 μ wide and thin-walled.

Hymenium. Basidia 26-34 × 11-16 μ, clavate, sterigmata short, 2-, or 3-spored (possibly some 4-spored). Cystidia or conidiophores (36-) 44-66 (-80) × 8-15 μ, the long ones are the narrowest, ventricose at base and with a long neck often irregular in outline, thin-walled, hyaline in KOH.

Hyphal layers. Mediostratum of tramal plates a broad band of subparallel to slightly interwoven hyphae 6-10 μ diam. and with sphaerocysts up to 25 μ scattered in it especially where plates branch; hymenopodium about 2 strands of parallel hyphae which are hyaline and thin-walled and give rise to diverging branches 2-3 cells long (the subhymenium) with the basidium arising as the terminal cell. Peridium as revived in KOH with ochraceous-walled filaments forming a thin epicutis of appressed hyphae; context of hyaline heteromerous tissue. Clamp connections absent.

On exposed soil along a logging road in rich heavy soil (mud), Ithaca, Michigan, Sept. 17, 1949, Victor Potter 8898, (MICH).

The elements of the spore ornamentation do not show any truly distinct amyloid spot at or near their apices. The elements are actually readily deciduous and with a little pressure on the cover glass can be broken off and studied in detail. The wall is pseudoamyloid clear to the apex in most warts and spines, and in others the intensity of the color diminished to yellowish, but in no case was a bluish spot or zone present. In observations on spores with the ornamentation in place, shadows occasionally give the effect of a dark spot, and at first these were regarded as possible amyloid areas.

The basidia with sterigmata showed small, rather narrow sterigmata, much narrower than the "sterigmal appendage" seen on many spores. This posed a question: Were some of the spores actually conidia instead of basidiospores? We suspect this to be true but were unable to demonstrate a spore attached to the apex of one of the "cystidia" or any other hymenial element. We consider it significant, however, that the width of the neck of the cystidia seen, and the thickness of the wall, corresponds to the same characters as observed on the sterigmal appendage of the spores.

Zeller & Dodge indicate a latex for *Arcangeliella asterosperma* var. *asterosperma*, but the Potter collections did not show one. This character and the completely inamyloid spores are the characters by which variety *potteri* is recognized.

8. Octavianina **nigrescens** (Zeller) Singer & Smith comb. nov.
Hydnangium nigrescens Zeller. Mycologia 40:641. 1948.
Fig. 8.

Gastrocarp 25-40 × 10-30 mm, subglobose to oblong or irregular, attached by a single rhizomorph, surface soft, glabrous, with some innate veins especially below, white, soon blackening, drying fuscous brown; gleba cinnamon brown, drying a slightly darker brown but remaining distinctly cinnamon, cavities distinct, "empty", columella and sterile base none.

Spores 12-16.5 × 10-14 μ, globose to broadly ellipsoid, with a thick inner wall (about 2 μ thick) which is *tawny in KOH and Melzer's;* exterior to this is a second layer which is also colored (pale tawny to ochraceous-tawny in KOH and Melzer's) and which is irregularly areolate-cracked into a number of large irregular warts with numerous fine striations; plage area not distinctive; sterigmal appendage short and typhal-like.

Hymenium continuous. Basidia 20-24 × 10-14 μ, short-clavate, hyaline, thin-walled, readily collapsing, 2-, 3-, and 4-spored; sterigmata straight, irregular and often hyphal-like, (typically gastroid); spores borne acropetally. Pseudoparaphyses numerous, 12-18 × 10-15 μ, hyaline, thin-walled. Cystidia none.

Hyphal layers. Subhymenium of branched filaments 4-7 μ diam. and subgelatinous as revived in KOH, hyaline and thin-walled; mediostratum of subparallel-interwoven non-gelatinous hyphae with thin smooth walls and hyphal cells equal in diameter or slightly inflated (3-12 μ diam.), no sphaerocysts present. Epicutis of peridium of appressed rusty brown hyphae (in KOH) 3-7 μ diam. rather closely interwoven. Context of interwoven hyaline hyphae about like those of the mediostratum of the tramal plates. Clamp connections none. Laticiferous or oleiferous hyphae none.

Partially exposed, on ground in mixed woods. Near Ithaca, New York, Tompkins County. Rogerson 1615, type (NY).

The type has been studied and appears to us to be an extreme spore-type in the genus *Octavianina*. The fine striae on the elements of the ornamentation in this species find their counterpart on the spores of such species as *O. lutea*, *O. laevis*, and *O. lanigera*. The color change of the fresh peridium is not out of line with that of *O. asterosperma*, and the color of the dried gleba is typical for the genus. The most interesting feature is the high degree of pigment development in the spores. If one has not studied the spores of the other species of the genus, he is likely to insist that by spore color this species is more properly referred to the series of gastromycetes connected to the Cortinariaceae of the Agaricales, but the structure of the outer wall is anomalous for this group. Actually, the spore color is merely a darker tone of the same type as observed for most others of the genus in which the tint ranges from hyaline to cinnamon buff in the darkest spores.

9. Octavianina **rogersii** Singer & Smith sp. nov.
Figs. 7 & 22.

Carpophoris 1-2.5 cm latis, subglobosis, albidis, impolitis, demum areolatis; gleba cinnamomeo-alutacea, loculis minutis; sporis 14-19 μ, subglobosis; pseudocystidis 60-80 × 7-11 μ. Specimen typicum legit prope Woods Creek, Benton Co. Oregon, U.S.A., 24 Mai 1939, D. P. Rogers (NY).

Gastrocarp 1-2.5 cm broad, globose to subglobose, flattened or quite irregular in outline, white when fresh and drying whitish to pale buff, surface unpolished as dried; peridium continuous or at times breaking into a number of lobes and gleba exposed above (not at base in any specimens seen so far). Gleba of minute chambers and drying nearly

"cinnamon buff", not of a gelatinous consistency. Columella as seen in dried material rudimentary to lacking, when present consisting merely of thin short lines of sterile tissue and not percurrent. Stipe absent.

Spores subglobose, 14-19μ diam., wall about 2 μ thick and pale orange-yellow in Melzer's reagent; sterigmal appendage absent to very inconspicuous and its walls thin and parallel (hyphal-like); ornamentation in the form of distinct rods and spines 1.5-3 × 0.6-1 μ, typically *pale yellow* in Melzer's reagent (spores from dried specimens) but a few seen with a distinct small bluish spot in upper half or at apex (for taxonomic purposes non-amyloid), the spines closely arranged but separate, no distinct plage area showing.

Hymenium. Basidia 42-56 × 10-15 μ, clavate, 1-spored, thin-walled, hyaline. Basidioles numerous, 30-38 × 9-11 μ. Pseudoparaphyses present as broadly inflated basidioles (10-15 μ broad), thin-walled, hyaline, readily collapsing. Cystidia scattered, 60-80 × 7-11 μ, narrowly clavate to narrowly fusoid, some with refringment rods and granules in interior, arising from oleiferous hyphae, thin-walled, hyaline in KOH.

Hyphal layers. Subhymenium of slightly enlarged to sphaerocyst-like cells, hyaline, thin-walled; mediostratum of filamentose hyphae with some oleiferous hyphae and some scattered sphaerocysts, all hyaline in KOH. Epicutis of peridium continuous with context and of appressed-interwoven narrow (2-4 μ) hyaline thin-walled smooth hyphae. Context mostly of interwoven filamentous hyphae but some sphaerocysts present near subhymenium. Clamp connections absent.

Under Douglas fir, Woods Creek road, Western Benton County, Oregon, May 24, 1939. Coll. D. P. Rogers.

This collection reminds one strongly of *Martellia monticola* but is at once distinguished by the essentially non-amyloid spores. The large 1-spored basidia are an outstanding feature, but one possibly not too reliable as a taxonomic character. The cystidia are *Russula-like* (pseudocystidia ?) and are a good character for the species. In gross morphology, in spore characters, and in the reduction in the number of sphaerocysts this species is to be regarded as below the level of *Martellia* in the evolutionary series. In the exceedingly weak amyloid reaction of the spores, it is, however, reminiscent of that genus. This reaction was noted on dried material revived in Melzer's reagent but did not show on material preserved in liquid and mounted in Melzer's fluid.

10. Octavianina **papyracea** Singer & Smith sp. nov.
Fig. 15.

Carpophoris 1-4 cm latis, subglobosis, albidis; gleba alutacea, locellis minutis; peridio papyraceo; latice cremoricolor; viscoso; sporis 14-17 μ, globosis, inamyloideis; sphaerocystibus in tramate nullis; hyphis defibulatis. Specimen typicum legit prope Trinidad, Calif. Nov. 21, 1939. H. E. Parks *6347* (NY).

Gastrocarp 1 cm diam., brownish, hard, globose, unchanging, color creamy; gleba of minute chambers, near pinkish-buff as dried and when moistened with alcohol orange-tan, with an abundant cream colored latex fresh, taste mild; columella lacking; peridium as dried almost like a

thin nut shell, the exterior surface dull cinnamon is some places and near cinnamon-buff in others.

Spores 14-17 μ, globose to subglobose, sterigmal appendage inconspicuous, spore wall thick (1 μ or more), in Melzer's reagent orange-yellow; ornamentation in the form of spines 2-3 μ long and 0.5-1 μ at the base, densely covering the surface but not fused, yellowish in Melzer's or nearly hyaline at tip; spore wall hyaline to yellowish in KOH.

Hymenium. Basidia 20-32 × 9-13 μ, thin-walled and readily collapsing, hyaline or nearly so in KOH, 1-, and 2-spored, sterigmata 10 μ or more long; cystidia a few seen, 46-60 × 10-13 μ, thin-walled, hyaline, soon "empty", subcylindric to enlarged near apex and with an apical mucro.

Hyphal layers. Mediostratum of tramal plates of interwoven, hyaline subgelatinous hyphae with slightly thickened walls, no sphaerocysts present; subhymenium of cells 10-13 μ in diam. in rows of 2-3 and rows terminated by a basidium or basidiole, all tramal tissues yellowish hyaline in Melzer's reagent. Epicutis of peridium a layer of appressed, ochraceous hyphae (in KOH) with some free hyphal ends at surface as a rudimentary turf; hyphal ends 3-4 μ diam.; context of hyaline subgelatinous hyphae with slightly thickened walls (similar to those of the tramal plates), interwoven; laticiferous hyphae present; sphaerocysts none; clamp connections none.

Under Sequoia debris but not buried in the soil, Spruce Cove, Trinidad, Calif. Nov. 21, 1939. H. E. Parks. The specimen is No. 6347 in the Zeller Collections (NY).

Parks (No. 5702) made a second collection which appears to be the above species, on Nov. 28, 1935 at Trinidad, Calif. It was hypogeous in an old road and under alder leaves but *Sequoia* was present in the vicinity also. The following data were recorded for this collection.

Gastrocarp 2-4 cm diam. globose or neary so; peridium creamy to ivory when fresh, becoming rufous at base where exposed, drying tawny; gleba slightly lighter in color, exuding a thick sticky cream colored latex when fresh and cut open. As dried the gleba is about cinnamon buff and the peridium nearly russet. No evidence of a columella was seen on cut specimens.

Spores 13-16 μ, globose, pale ochraceous in KOH, darker ochraceous in Melzer's reagent (but not pseudoamyloid), sterigmal appendage short and inconspicuous; ornamentation in the form of cones 1-2 μ high and 0.5 μ at base, non-amyloid or with faint "shadows" near apex in some; wall thickened somewhat.

Hymenium. Basidia 25-32 × 9-12 μ, clavate, hyaline in KOH, a few seen with 4-6 very fine sterigmata. Cystidia about 50-65 × 10-16 μ and pointed but very badly collapsed, rare (but probably more numerous than the observations indicate).

Hyphal layers. Tramal plates with interwoven hyaline hyphae and large laticiferous hyphae, no sphaerocysts found; subhymenium of divergent hyphae with basidia at the ends but divided below the basidium into 2-3 short cells which enlarge to 8-13 μ. Epicutis of pileus a narrow ochraceous (in KOH) layer of appressed subgelatinous hyphae, context of

hyaline glassy (in KOH) hyphae 5-8 μ in diam., and laticifers but no sphaerocysts. Clamp connections none.

The latex-bearing and non-latex bearing species are so closely related in their other characters that at this level we have been unable to convince ourselves that they should be placed in separate genera. The papery-fragile peridium is distinctive of the holotype and undoubtedly is a good "herbarium" character.

11. Octavianina tuberculata (Hesse) O. Kuntze, Rev. Gen. Pl. 3²:501. 1899.

Hydnangium tuberculatum (Hesse) Zeller & Dodge, Ann. Mo. Bot. Gard. 22:373. 1935.

Octaviania tuberculata Hesse Hypog. Deutsch. 1:75-77. 1891. Fig. 10.

Gastrocarp 13 × 20 mm, subglobose, more or less warty and uneven and also furrowed, white at first, yellow where handled, finally brownish; gleba marbled, tramal plates showing pallid against the cavities which are filled with dark brown spores; columella and sterile base none. Odorless.

Spores 12-16 μ, globose, covered with broad cones 2-3.5 × 2-3 μ, dark reddish brown in Melzer's reagent, the wall of the cones usually with at least a few longitudinal striations or creases, color in KOH near ochraceous tawny; plage area not different from remainder; sterigmal appendage usually not visible. Not amyloid in any part; inner wall thick and pale tawny.

Hymenium continuous. Basidia 18-22 × 10-14 μ, broadly clavate, thin-walled, readily collapsing (3-4-spored, Zeller & Dodge). Basidioles present; pseudoparaphyses ellipsoid, 12-15 μ broad. Cystidia none seen.

Hyphal layers. Subhymenium of inflated sphaerocyst-like cells, hyaline, thin-walled; mediostratum of hyaline slightly interwoven filaments. No sphaerocysts seen in the layer but some slightly inflated cells present, all hyphae thin-walled and smooth. Epicutis not differentiated from context, entire peridium of interwoven filaments 8-13 μ in diam., hyaline, thin-walled and no true sphaerocysts present. Clamp connections none.

Under *Fagus sylvatica*, Hessen-Nassau, Germany, September and October, 1888. Specimen collected and identified by Hesse (Zeller Herbarium, NY).

The warty surface of the gastrocarp appears to be a good field character, at least it has been found constant in other genera in this series. The staining to yellow of the injured surface should be a second distinctive character and helps to separate it from the other species described by Hesse.

12. Octavianina lutea (Hesse) Singer & Smith comb. nov.

Octaviania lutea Hesse. Pringsh. Jahrb. f.w. Bot. 16:255. 1885.

Hydnangium luteum (Hesse) Zeller & Dodge, Ann. Mo. Bot. Gard. 22:372. 1935.

Fig. 11.

Gastrocarp 2.5-3 cm thick, subglobose to irregular, snow white when young and fresh, gradually becoming dingy but retaining white patches, when handled or injured turning red, finally cherry red. Gleba when first sectioned (young specimen) snow white, but soon changing to red-

dish, in old specimens when cut the surface shiny and golden yellow. Sterile base rudimentary in young specimens, obsolete in age. Odorless.

Spores 14-19 μ, globose, ornamented with broad pyramids 2.5-3 × 2-2.5 μ, spores yellowish in KOH, dark rusty brown in Melzer's sol. thick-walled (the *O. asterosperma* - type).

Hymenium. Basidia short-clavate, 23-27 × 10-15 μ, 2-, 3-, 4-spored, hyaline, thin-walled, readily collapsing. Pseudoparaphyses clavate, those observed by Smith more broadly clavate, about 20 × 9 μ, with *slightly thickened walls* (as illustrated by Hesse). Cystidia none.

Hyphal layers. Subhymenium filamentous, of broad cells (6-10 μ). Mediostratum of filamentous hyphae mostly rather broad (7-10 μ), and some of the cells appreciably inflated (sphaerocysts ?) all hyphae hyaline in KOH and readily disintegrating under pressure. Epicutis of appressed filamentous hyphae nearly hyaline in KOH and 3-8 μ in diam. Context of hyaline thin-walled hyphae of both narrow and broad types (3-10 μ diam.). Presence of sphaerocysts doubtful; clamp connections none observed but conclusion not final.

The specimen studied was collected by Hesse under birch at Altmorschen, Hessen, Nassau, Germany, September 1889. (Zeller Herbarium, NY).

The peridium remained pallid on drying and easily sloughs off. The gleba is cinnamon as dried. The white peridium which stains cherry red on handling and the golden yellow gleba at maturity appear distinctive.

13. Octavianina lanigera (Hesse) O. Kuntze, Rev. Gen. Pl. 3²:501. 1898.
Octaviania lanigera Hesse, Hypog. Deutschl. 1:79-80. 1891.
Hydnangium lanigerum (Hesse) Zeller & Dodge, Ann. Mo. Bot. Gard. 22:372. 1935.
Fig. 12.

Gastrocarp irregular in shape, roughly 1-2.5 cm diam., often with a constriction dividing it into two lobes, or in some one of the lobes further divided, with a mycelial attachment in (at base of) the primary furrow, color yellowish white from a loosely fibrillose outer layer; peridium nearly 1 mm thick and not separable from the gleba but at maturity breaking up into small patches. Gleba golden yellow, of cavities of appreciable size partly filled with spores, pale cinnamon as dried; columella (none evident in specimen examined), sterile base very inconspicuous in dried specimen. No appreciable odor.

Spores 11-16 μ; globose, of coarse spines and warts about 2-3 × 2-2.5 μ, ornamentation non-amyloid; spore rusty brown in Melzer's, ochraceous in KOH (obviously the *O. asterosperma* type).

Hymenium of very delicate-walled elements all readily collapsing. Basidia 4-spored, 20-22 × 10-12 μ, thin-walled, hyaline. Cystidia none observed. Basidioles numerous. (Hesse, fig. 7 l.c. shows some thick-walled, 2-celled elements in the hymenium about the size of basidioles).

Hyphal layers. Tramal plates of interwoven hyaline subgelatinous hyphae 5-11 μ in diam. and readily disintegrating when revived; a few cells observed which might be interpreted as sphaerocysts; subhymenium of filamentous-hyphae about like those of the mediostratum. Epicutis of gastrocarp of hyaline to pale yellowish interwoven thin-walled hyphae 8-

11 μ diam. Context of loosely interwoven hyphae about like those of the outer layer but some sphaerocysts possibly present ("holes" in the inner context may mark the occurrence of collapsed sphaerocysts). Clamp connections, none observed after considerable study. Oleiferous hyphae rare.

The specimen studied was collected by Hesse under Betula, Altmorschen, Hessen-Nassau, Germany, Sept. 1901. (Zeller Herb. NY).

This species is congeneric with *O. asterosperma* and *O. laevis* by its spore characters, but distinct from both by the characters of the peridium.

14. Octavianina laevis (Hesse) Kuntze. Rev. Gen. Pl. 3²:501. 1898.
Octaviania laevis Hesse, Hypog. Deutschal. 1:80-81. 1891.
Arcangeliella laevis (Hesse) Dodge, Ann. Mo. Bot. Gard. 22:368. 1935.
Hydnangium laeve (Hesse) Zeller & Dodge, Ann. Mo. Bot. Gard. 22:372. 1935.
Fig. 13.

Gastrocarp 1-2 cm in diam., globose to slightly irregular in shape, surface smooth and silky-fibrillose, whitish, gradually becoming brownish, and when dried dark rusty brown; gleba whitish becoming yellow and when dried pale cinnamon, chambers extremely minute (scarcely visible to unaided eye); columella none; sterile tissue none; odorless.

Spores globose 13-18(20) μ in diam.; strongly ornamented with cones 2-3 × 2-2.5 μ; non-amyloid to pseudo-amyloid, (rusty brown in oldest or largest spores in Melzer's reagent), walls of cones rusty brown below, yellow near apex, cones so closely spaced as to touch each other at base; spore color in KOH pale ochraceous.

Hymenium of very delicate-walled elements readily collapsing. Basidia about 10-12 μ broad, nearly globose, 2-, and 4-spored, walls *very* thin and hyaline. Basidioles present but remaining badly collapsed; cystidia none.

Hyphal layers. Tramal plates of interwoven gelatinous narrow (2-3 μ) hyaline hyphae; no sphaerocysts found; subhymenium scarcely distinct in revived mounts—apparently of the same type of subgelatinous hyphae composing the mediostratum. No oleiferous or laticiferous hyphae seen. Epicutis of peridium of filamentous, appressed, interwoven hyphae with rusty brown pigment in the layer but individual hyphae as isolated have merely slightly ochraceous walls. Context of peridium of subgelatinous interwoven hyphae hyaline in KOH; a few inflated cells seen which could be interpreted as sphaerocysts. Clamp connections none found.

The description is taken from the original by Hesse, and the microscopic data are from a Hesse collection made at Altmorschen, Hessen-Nassau, Germany, July 1888 by Hesse himself.

This is a species closely related to and congeneric with *O. asterosperma* (the spores are almost identical) but differs in the greater reduction of sphaerocysts in the context of the peridium, in different color changes when fresh specimens are handled, and in having more of a tendency for the hyphae of the tramal plates to gelatinize. Zeller's collection from Salem, Oregon, April, 1935 is correctly identified. It was found under *Opulaster* and *Corylus* (hazel). The Thaxter collection "B_2 H" from Burbank, Tenn. August 1896 is also correctly determined. Thus it is likely that Thaxters (B216) collection from North Carolina is correctly identified

also but we have not examined it. The distribution of the species in North America is thus widespread.

Zelleromyces gen. nov.

Carpophoris globosis, elongatis vel irreguleribus; sporis ornamentatis atque amyloideis; columellas manifesta; latice copioso; sphaerocystibus in peridio praesentibus.

Gastrocarp consisting of peridium, gleba and usually a well defined columella, the gleba chambered and cavities only partly filled with spores; spores with amyloid material over at least part of the basic ornamentation or ornamentation entirely amylaceous; peridium well developed, the epicuticular layer distinctive by virtue of being a trichodermium or at least with numerous dermatocystidia, usually the trichodermial elements arranged compactly so as to form an almost cellular epicutis; heteromerous tissue present at least at the junction of the tramal plates with the peridium; latex present in fresh material.

Type species. *Zelleromyces cinnabarina* Singer & Smith.

In its gross morphology this genus corresponds to *Martellia* but anatomically a greater range of characters is allowed. The spore ornamentation varies from only partly amyloid to the heaviest reaction we have seen in the whole series. There is also a wide range in the types of epicutis present on the peridium.

Since the presence or absence of sphaerocysts in the mediostratum of the tramal plates has been considered important at the generic level in *Macowanites* and *Elasmomyces* in the *Russula* branch of the Astrogastraceous Series, some comment on the situation as described here for *Zelleromyces*, is pertinent. *Z. cinnabarinus* and *Z. oregonensis* lack this character, whereas it is present to some degree in the remaining species. In fact, the genus might well be divided into sections on this character. We hesitate, however, to recognize two separate genera for these two groups because throughout the whole *Lactarius* branch of the Astrogastraceous Series, in fact in *Lactarius* itself, there is a general tendency for the mediostratum to lack sphaerocysts. In this particular situation we believe that the combination of lack of clamp connections, presence of amyloid spore ornamentation and presence of a latex is the best index of close relationship.

KEY TO SPECIES

1. Spores typically elliptic in profile view; sphaerocysts absent from mediostratum of tramal plates 2
1. Spores globose, or sphaerocysts present in mediostratum 3
2. Peridium cinnabar red fresh; spores 14-17 × 11-13 μ. . . . . 15. *Z. cinnabarinus*
2. Peridium pale cream color to pale clay color fresh; spores 10-13 × 8-11 μ. . . . . 16. *Z. oregonensis*
3. Peridium with a medial gelatinous layer with heteromerous tissue to the interior of it . . . . . 17. *Z. ravenelii*
3. Not as above, i.e., no heteromerous tissue present in the peridium, if a peridium is present 4
4. Spores globose 10-15(16) μ, ornamentation in form of spines with the apex amyloid . . . . . 18. *Z. gilkeyae*

4. Spores globose 9-12 μ diam., ornamentation of broad warts entirely covered by amylaceous material ..... 19. *Z. glabrellus*
4. Spores broadly ellipsoid 9-12.5 × 6.5-8.5 μ ornamentation in the form of ridges and crests ..... 20. *Z. gardneri*

15. **Zelleromyces cinnabarinus** Singer & Smith sp. nov. Fig. 16.

Carpophoris 1-4 cm latis, globosis, cinnabarinis; latice albido; sporis 14-17 × 11-13 μ, ellipsoideis; reticulatis, amyloideis; cystidiis 26-30 × 9-13 μ rarisuscnlis. Specimen typicum legit prope Jackson, Louisiana. U.S.A., 26 Dec. 1931. A. H. Smith & C. A. Brown (MICH).

Gastrocarps 1-4 cm in diam., globose, flattened or somewhat irregular in outline, sessile but attached by a mycelial pad, dull cinnabar red when fresh, drying dark reddish brown; gleba pale cinnamon to dull cinnamon-buff, chambered, chambers empty, irregular in shape but generally radiating out to peridium in an obscure pattern (most noticeable near point of attachment); columella rudimentary to absent, branched and branches radiating from the slight sterile base; when cut exuding a white latex.

Spores 14-17 × 11-13 μ, ellipsoid, ornamentation strongly amylaceous, forming a knotty reticulum, prominences about 1μ high, bands of amyloid material 0.6-1 μ wide; spore wall hyaline or nearly so in Melzer's reagent, with an irregular sterigmal appendage 2-4 μ long with some amylaceous material on it.

Hymenium. Basidia 20-26 × 9-12 μ, mostly 2-spored, hyaline, thin-walled, collapsing. Cystidia 26-30 × 9-13 μ, broadly fusoid to ovate-pointed and some with refractive content, rather rare.

Hyphal layers. Tramal plates of interwoven filaments and laticiferous hyphae; subhymenium appearing cellular in section (but actually of compactly interwoven filaments with cross walls so numerous as to produce isodiametric cells), giving off branches on which the basidia and basidioles occur, these branches having one or two short cells below the hymenial element. Epicutis of peridium a tangled layer of elavate cells, enlarged hyphal cells and some filaments all subgelatinous in KOH and difficult to revive. Laticiferous hyphae present. Sphaerocysts in context scattered, hence context weakly heteromerous. Clamp connections absent.

Under young pine, Jackson, Louisiana, (near Baton Rouge), Dec. 26, 1931, A. H. Smith and C. A. Brown.

This species was at first identified as *Arcangeliella ravenelii* but is readily distinguished by its distinctly ellipsoid spores and cinnabar-red peridia. As preserved the gastrocarps are a darker redder brown than those of *Z. ravenelii.*

16. **Zelleromyces oregonensis** Singer & Smith sp. nov. Fig. 17.

Carpophoris 10-30 mm latis, globosis, pallide alutaceis; latice albido; sporae 10-13 × 8-11 μ, echinulatis, amyloideis; cystidiis 46-48 × 9-11 μ. Specimen typicum legit. prope. Comstock, Ore. U.S.A., 23 Oct. 1937, S. M. Zeller, *N. 8333* (NY).

Gastrocarp 10-30 mm broad, globose, cinnamon-buff to dingy pale tawny as dried, surface unpolished; columella dendroid, branches pale buff; gleba "marbled with hygrophanous translucent areas"—Zeller. Chambers small

but labyrinthiform, cinnamon buff to pale ochraceous tawny (as dried); peridium thin, not opening to expose the gleba; "milk clear, whitish"—Zeller.

Spores 10-13 × 8-11 μ, subglobose to broadly elliptic, sterigmal appendage inconspicuous, about 2.5-3 μ long, ornamentation in the form of closely set but unconnected rods 1-1.25 × 0.4-0.5 μ; in some spores the rods arranged in crescents or in chains and touching or almost touching each other, amyloid over all or just over the upper two thirds, the rods rather readily deciduous, plage area ornamented but the elements reduced merely to amyloid granules; spore wall only slightly thickened and hyaline in Melzer's reagent.

Hymenium. Basidia 32-44 × 9-14 μ, 4-spored, clavate-pedicellate, thin-walled, collapsing readily; cystidia 46-48 × 9-11 μ, fusoid-ventricose to subcylindric or narrowly clavate, apex obtuse, rare to scattered and content protoplasmic, evenly refractive as revived in KOH (not macrocystidia).

Hyphal layers. Tramal plates with a mediostratum of interwoven hyaline (in KOH) hyphae 5-12 μ in diam.; the subhymenium cellular, 1-2 cells deep and elements up to 18 μ broad (sphaerocysts ?). Epicutis of peridium a turf of dermatocystidia, the elements 28-45 × 4-9 μ, narrowly subfusoid to filamentose, the walls slightly thickened in some, hyaline to yellowish in KOH, smooth, rarely with refractive content of amorphous material; context of interwoven filaments, sphaerocysts rare and present near the subhymenium in groups of 2-3, hypodermal layer yellow in KOH, the pigment in the hyphal walls, this zone of more compactly arranged hyphae than that making up the body of the context; laticiferous hyphae present but very scattered; clamp connections absent.

Under incense cedar, Comstock, Oregon, Oct. 23, 1937, S. M. Zeller, 8333.

This was identified as *Arcangeliella cremea* by Zeller, but differs from that species in the characters of the epicutis of the peridium, the shape of the cystidia, and in the more uniform elements of the spore ornamentation. Zeller specifically mentioned the latex (milk) for this collection. The absence of a latex in the type of *A. cremea* is inferred because it was not mentioned in the original description. This could be an erroneous assumption but we doubt if it is. Sprague, who collected the type of *A. cremea* at Corvallis, Oregon, no doubt gave the fresh material to Zeller, who then, as was his habit, sectioned it and thus would have observed a latex if one had been present.

17. **Zelleromyces ravenelii** (B. & C.) Singer & Smith comb. nov.

Octaviania stephensii var. *ravenelii* Berk. & Curt. in Tulasne, Fung. Hypog. xvii. 1851.

Hydnangium stephensii var. *ravenelii* Berkeley, Grevillea 2:33. 1873.

Octaviania ravenelii Lloyd, Myc. Notes 67:1140. 1922.

Arcangeliella ravenelii (B. & C.) Dodge, Ann. Mo. Bot. Gard. 18:463. 1931.

Fig. 18.

Gastrocarps 25-40 mm in diameter, subspherical to pyriform, drying light fawn to nearly pallid; sterile base not prominent; columella slender, percurrent; with laticiferous ducts which exude a white aromatic latex.

Spores 12-16(17) μ, globose or nearly so, ornamented, blackish violet under oil-immersion in Melzer's reagent because of a heavy ornamentation in the form of a small-meshed reticulum of ridges about 1 μ wide connected by finer amyloid lines or chains of granules, main ridges 1-1.5 μ high and secondaries about 0.25 μ high; sterigmal appendage inconspicuous.

Hymenium. Basidia 2-spored, a few 1-spored with an elongated sterigma or intermediate (one long and one aborted), basidia 36-45 × 10-13 μ, sterigmata on two-spored basidia 9-12 μ long and 2 μ wide at base, conic. Basidioles numerous. Cystidia 48-60 × 10-15 μ, clavate with an apical mucro but mostly larger than 1-spored basidia.

Hyphal layers. Subhymenium cellular but not from sphaerocysts, merely of short cells more or less isodiametric because of numerous cross walls; hyphae of the tramal plates interwoven and hyaline with scattered sphaerocysts. Peridium a thick (about 200 μ) layer of hyaline subgelatinous hyphae 4-11 μ in diam. with laticiferous hyphae interspersed, covering the surface sparsely are small dermatocystidia 18-26 × 3-7 μ, these are irregular in outline. Clamp connections absent.

Material studied. Ravenel, Fungi Amer. N.16, Ellis, N.A.F. no. 1211.

The white latex with an aromatic odor in combination with the heavy reticulum of the globose spores furnishes a good combination of characters by which to recognize this species. In fact it is exceptionally well characterized. The Zeller collections from Oregon have a peridium reminding one of a *Scleroderma*, but the large dark, amyloid spores with their heavy reticulum are like those of the Ravenel collections.

18. **Zelleromyces gilkeyae** Singer & Smith sp. nov.
Fig. 19.

Gastrocarpis 20-35 mm latis, rugulosis, rubro-brunneis; gleba pallide alutacea, molli; latice albo. Sporis 10-15(16) μ, globosis; cystidiis 46-62 × 10-14 μ. Specimen Typicum in Herb. "N.Y." conservatum est. legit prope Reedsport, Ore., 22 Oct. 1938. Sub *Acer circinatum*, Helen Gilkey, *Zeller 8498*. (NY).

Gastrocarps 20-35 mm broad and about 2 cm deep, surface pale reddish brown and wrinkled; gleba cinnamon-buff; consistency rather punky and gleba readily attacked by insects in the herbarium; no stipe or columella visible (data on dried material). Miss Gilkey reported a columella when fresh and a white latex.

Spores globose, 10-15(16) μ, ornamentation in the form of rods and spines 2-3 × 0.7-1 μ (long and narrow), and these slightly amyloid near or at the apex, and also in most spores with a darker amyloid reaction around the base or near it, spines closely arranged but no connecting ridges between them, and the wall of the spore between them merely yellowish in Melzer's reagent and in KOH merely yellowish-hyaline.

Hymenium. Basidia 2-spored, 30-37 × 9-12 μ, (possibly a few 4-spored); basidioles 20-35 × 9-11 μ. Pseudoparaphyses none. Cystidia abundant, 46-62 × 10-14 μ, elongate-mucronate, thin-walled, hyaline in

KOH or with scattered refractive amorphous particles within, or content reticulate.

Hyphal layers. Subhymenium cellular, mediostratum of interwoven filaments and laticiferous hyphae, scattered sphaerocysts also present. Peridium with an outer layer in the form of a trichodermium with the elements so closely packed together as to form a cellular layer, the end-cells ochraceous brown in KOH; beneath this layer is one of interwoven subgelatinous hyphae (no sphaerocysts reliably observed); clamp connections none but false clamps occasionally present.

Under *Acer circinatum* in deep mixed woods, near Reedsport, Oregon, October 22, 1938. Zeller 8498, collected by Dr. Helen Gilkey.

In the Zeller collections this number was filed as *Arcangeliella occidentalis*. We do not question that a columella was present in at least most of the specimens. Miss Gilkey's notes leave no doubt on that score, but it does not show in the cut specimens available for study. This we explain as an artifact and would point out that Smith has noted the same thing happening in some of his collections in this group.

This species is distinct because of the large spores with localized amyloid material on the main spines of the ornamentation, the large cystidia of the macrocystidium type, and the structure of the epicutis of the peridium. We strongly doubt if this is the fungus Harkness described as *Octaviania occidentalis* from under oak in California. McMurphy No. 272, March 23, 1919, also labeled *A. occidentalis* in the Zeller collections is still a different species having a thick gelatinous layer over the exterior of the peridium, and it lacks cystidia, among other characters.

The localized amylaceous material on the spines of the spore ornamentation, the almost cellular epicuticular trichodermium, and the cystidia remind one of *Martellia*, but the presence of a latex excludes that genus.

19. **Zelleromyces glabrellus** (Zeller & Dodge) Singer & Smith comb. nov.
Arcangeliella glabrella Zeller & Dodge, Ann. Mo. Bot. Gard. 22:368. 1935.

Fig. 20.

Gastroearps 10-15 mm in diam., drying to 5-10 mm, subglobose to depressed-globose, smooth, white to brownish, drying sordid white to buckthorn-brown; columella percurrent; gleba white, drying ivory-yellow to cream-buff, cavities nearly spherical; latex present.

Spores globose, 9-12(13) μ, so strongly amyloid as to be blackish violet and opaque in Melzer's reagent and the ornamentation difficult to measure (but about 1-1.5(2) μ high and each element almost as broad at the base as it is high), in the form of warts and obtuse cones; sterigmal appendage inconspicuous to absent.

Hymenium. Basidia 4-spored, clavate, 36-45 × 10-13 μ, sterigmata straight, 4-5 × 2 μ; pseudoparaphyses present, 12-16 μ broad, thin-walled and readily collapsing. Cystidia abundant and voluminous, 50-70 × 14-20 μ, broadly fusoid, thin-walled, content homogeneous in KOH, smooth, readily collapsing, rarely some slender cystidia with amorphous contents (pseudocystidia) in KOH also present.

Hyphal layers. Tissue of the tramal plates heteromerous, sphaerocysts rare in the thin plates, and a few in the cellular subhymenium. Peridium

with an epicutis of the type found in Lacrymaria of *Psathyrella* in the Coprinaceae (Agaricales), i.e., cellular and 2-4 cells deep with filaments projecting between the cellular elements, all parts hyaline in KOH and thin-walled; beneath the epicutis is a layer of filamentous hyphae 4-8 μ in diameter but no sphaerocysts were seen (the layer revived poorly), no true laticiferous hyphae were seen (the structures observed were more like oleiferous hyphae in morphology, but apparently carried a latex). Clamp connections none.

This species is based on a collection from Tasmania by Rodway (his number 1111).

Among the Zeller collections is a portion of the type collection consisting of two gastrocarps, one slightly smaller than the other. We have selected as the lectotype the specimen which is small and would have been the one referred to as a young fruiting body. It shows cystidia and was apparently the element in the collection seen to have the latex. This makes the type consistent with the outstanding diagnostic characters as given in the original description.

The second (the larger) specimen we have not as yet identified. In it the peridium shows obvious heteromerous tissue, it has no obviously differentiated epicutis, the spores are globose to ellipsoid, 9-11 × 8-10 μ, and with ornamentation 0.25 μ high consisting of scattered warts, granules and some crests which are mostly unconnected. The basidia are 2-, 3-, and 4-spored, 26-33(44) × 9-11 μ, and pseudoparaphyses 12-18 μ broad are present but cystidia are lacking. Sphaerocysts are present in at least the thicker tramal plates but these structures revived poorly. Clamp connections are absent.

It was obvious when working with the specimens that each was fully expanded and mature. Hence the characters are comparable. It should also be pointed out that the spores in neither of the gastrocarps correspond in size with the measurements given by Zeller & Dodge. Is there still another species hiding in Rodway 1111? As we have typified *Z. glabrellus* it is readily recognized by the extremely dark amyloid reaction of the heavy spore ornamentation, the cystidia and the structure of the epicutis. It is placed in *Zelleromyces* on the assumption that it was this element in the collection which exuded a latex. From the fact that the original description calls for a latex in the "young specimens" we question whether the other elements of the collection however many these are, actually had a latex.

20. **Zelleromyces gardneri** (Zeller & Dodge) Singer & Smith comb. nov.
Gymnomyces gardneri Zeller & Dodge, Ann. Mo. Bot. Gard. 6:54-55. 1919.
Arcangeliella gardneri (Zeller & Dodge) Zeller & Dodge, Ann. Mo. Bot. Gard. 22:367. 1935.
Fig. 21.

Gastrocarp subglobose to irregular, depressed, 25 × 15 × 15 mm drying out to 14 × 8 × 8 mm, cream colored to yellow ochre in alcohol, drying tawny olive; columella dendroid, resembling much thickened septa; gleba cream color to clay color dried, cavities small, isodiametric to irregular; latex white.

Spores 9-12.5(15) × 6.5-8.5(-10) μ, broadly ellipsoid to subglobose, ornamentation strongly amyloid, 0-25-0.5 μ high and in the pattern of crooked ridges, warts fused into crests and these connected to give the effect of a broken reticulum; nearly hyaline in KOH; sterigmal appendage very inconspicuous (about 2 μ long.)

Hymenium. Basidia 4-spored, 26-37 × 7-9 μ, clavate, thin-walled and readily collapsing, sterigmata very fine and straight-conic. Pseudoparaphyses clavate, 20-25 × 10-12 μ (basidioles ?) cystidia 24-35 × 10-16 μ, ellipsoid-mucronate, thin-walled, readily collapsing, content homogeneous or nearly so, (hence not chrysocystidia).

Hyphal layers. Tramal plates with hyphae reviving poorly but some sphaerocysts clearly demonstrated in the mediostratum—hence the tissue at least weakly heteromerous. Subhymenium cellular, cells about the width of the base of the basidium. Peridium (very little present, the surface being alveolate as in *Gautieria*), all that was evident under the microscope was a thin layer of appressed filaments of non-gelatinous hyphae. Laticiferous hyphae present. Clamp connections none.

Under leaves of *Quercus agrifolia*, California. December.

Material studied. The part of the type collection in the Zeller Herbarium (NY).

Among the Zeller Collections are the following identified as the above species. Parks No. Z-11. This is not the same as the type, but we are not prepared to identify it or describe it at present. Zeller No. 16 (Parks Z-2) is immature but apparently represents another species. Parks Z-348 represents a fourth species in which the prominent elements of the spore ornamentation are only partly amyloid. Murphy No. 271 by virtue of its cheese-like consistency when dried and small ellipsoid spores is still another species, but his 267 is possibly the same as his 271 though the spores are globose. Parks 943 appears to be the same as the type. It lacks a peridium, the surface as dried is somewhat alveolate, and the spores check reasonably well. We found no cystidia but are not inclined to emphasize this as a character at present. Zeller 1728, by H. P. Barss from Corvallis, Oregon, also appears to be correctly identified. Hence, *Z. gardneri* is known from 3 different localities, and the thin evanescent peridium appears to be constant. It is to be noted that in this species the spore ornamentation is very similar to that found in *Lactarius*.

MARTELLIA Mattirolo

Malpihgia 14:78-82. 1900.

Tissue of peridium entirely of filamentous hyphae or with scattered sphaerocysts or truly heteromerous in at least the inner layer; epientis of peridium various, consisting of a turf of dermatocystidia, or in the form of a cellular epientis, or epientis not clearly differentiated from the context; tramal plates with a distinct filamentose mediostratum lacking sphaerocysts; subhymenium typically of enlarged sphaerocyst-like cells; spores ornamented and the ornamentation amyloid over all or, for many species, only over a portion of the ornamentation; columella present or absent, if present often arising from a sterile base; latex absent and

laticiferous hyphae typically absent; oleiferous hyphae sometimes present. Clamp connections absent.

Type species. *Martellia mistiformis* Mattirolo.

As we have defined the genus it differs from *Hydnangium* in lacking clamps on the hyphae and in having some part of the spore ornamentation distinctly amyloid. The genus can readily be divided into three sections. Section *Protocystangium* characterized by a cellular peridial epicutis and a lack of sphaerocysts in the tissue of the peridium; section *Martellia* with sphaerocysts in the context of the peridium, and Section *Martelliella* in which sphaerocysts are not present in the peridial context and the epicutis of the peridium is relatively undifferentiated or present only as a turf of dermatocystidia.

Martellia in the sense that we have presented it here shows three interesting trends in development. First, the degree of development of sphaerocysts in the context of the peridium. The type of the genus is actually intermediate in this respect and in a way connects the group of species lacking these structures in the peridial context to the group which possess them. In the latter group occur species with scattered sphaerocysts and one in which these structures appear in pockets but are not greatly enlarged. In view of the highly developed heteromerous tissue in *Lactarius* and *Russula*, the degree to which sphaerocysts occur in the peridial context of *Martellia* is of the greatest interest.

The second line of development is in the extent of the coating of amyllaceous material over the elements of the spore ornamentation. The smallest indications of this character were observed in *Octavianina rogersii*, but we have not described that species in *Martellia* because for all practical purposes the spores are inamyloid. In *Martellia* it is possible to arrange a series of species starting from those with weakly developed or spotty amylaceous material on the elements of the spore ornamentation, as in *M. maculata*, to those evenly coated, but in those entirely covered by amyllaceous material there are some in which the element of ornamentation is deeper blue at the apex than elsewhere. It is also significant in this genus that as a genus the spores show many of the basic types of ornamentation described in the Singer (1951) system. Thus the development in the amyloidity of the spore ornamentation parallels roughly the development of the sphaerocysts.

The third line of development is in the epicutis of the peridium. In its most specialized form this layer occurs as a cellular epithelium reminding one of that of *Cystangium*. Indeed, if one is forced to postulate an origin for *Cystangium* it would be from this group of species. *M. idahoensis* has a peridium in which the epicutis approaches the type found in *Cystangium* and is to be regarded as an intermediate stage between a turf of dermatocystidia and a truly cellular type. In a number of species very little differentiation of the epicutis is found, a situation common in *Octavianina*. Thus, in all the major cellular and anatomical characters save one (sphaerocysts in the mediostratum of the tramal plates) leading to the Russulaceae we find them in a rudimentary condition in *Martellia* as well as stages showing considerable evolutionary progress in their specialization.

KEY TO SPECIES

1. Sphaerocysts absent from tissue of peridium 2
1. Sphaerocysts (or irregularly enlarge cells in *M. mistiformis*) present to some extent—often merely scattered—in the tissue of the peridium 15
2. Epicutis a layer of vesiculose cells 1-several deep 3
2. Epicutis a turf of dermatocystidia or not differentiated from context 6
3. Cystidia present in hymenium, fusoid ..... 21. *M. oregonensis*
3. Cystidia absent 4
4. Spore ornamentation in the form of warts, spines, ridges, crescents, or irregular "knotty" lines (all types present on a single spore) 22. *M. variabilispora*
4. Element of spore ornamentation not fused in above patterns, occurring as discrete warts and spines 5
5. Gastrocarp soon stained brown; spore ornamentation conspicuously spotty in its amyloid reaction (spore not evenly violaceous in Melzer's) 23. *M. maculata*
5. Gastrocarp white (gray as preserved in liquid); spore ornamentation evenly amyloid or sufficiently so to give the reaction an even appearance under ordinary magnifications ..... 24. *M. vesiculosa*
6. Spores mostly over 12 μ wide or if 9-12 μ wide then 10-14 μ long 7
6. Spores mostly less than 12 μ wide 11
7. Spores ellipsoid and 15-23 × 12-16 μ ..... 25. *M. ellipsospora*
7. Spores not as above 8
8. Spores ochraceous tawny in KOH but ornamentation amylaceous ..... 26. *M. soehneri*
8. Not with above combination of characters 9
9. Elements of spore ornamentation 1-2.5 μ broad at base, in the form of simple or forked spines or truncated cones 3.5-5 μ high ..... 27. *M. gilkeyae*
9. Not as above 10
10. Cystidia abundant in hymenium; gleba yellowish, dried ..... 39. *M. scissilis*
10. Cystidia absent in hymenium, gleba cinnamon brown as dried ..... 28. *M. parksii*
11. Basidia with distinct yellow, to orange or brown content in KOH 12
11. Basidia hyaline or nearly so in KOH 14
12. Ornamentation with elements 0.25-0.5 μ high ..... 29. *M. californica*
12. Ornamentation with elements higher than above 13
13. Cystidia present in hymenium; resembling chrysocystidia as revived in KOH 30. *M. fallax*
13. Cystidia absent ..... 31. *M. subfulva*
14. Cystidia present in hymenium, of the type termed Macrocystidia 32. *M. foetens*
14. Cystidia none, setalike dermatocystidia present ..... 33. *M. brunnescens*
14. No dermatocystidia present ..... 34. *M. albella*
15. Spore ornamentation mainly in the form of a broken reticulum 16
15. Spore ornamentation as discrete elements or 1-2 united into an irregular isolated ridge 17
16. Peridial surface plush-like; cystidia present in hymenium ..... 35. *M. setigera*
16. Peridial surface silky to unpolished; cystidia absent ..... 36. *M. monticola*
16. Pleuro cystidia present, surface of gastrocarp subgelatinous ..... 36a. *M. alba.*
17. Epicutis of pileus a thick layer of appressed gelatinous hyphae 37. *M. occidentalis*
17. Not as above 18
18. Epicutis of peridium of a compacted trichodermium; gastrocarp wrinkled when fresh ..... 38. *M. idahoensis*
18. Epicutis of peridium of appressed filaments 19
19. Odor of fresh specimens strong of witch hazel; spines of spore ornamentation amyloid only at the tip 39. *M. scissilis*
19. Odor not distinctive; spore ornamentation heavily amyloid 40. *M. cremea*
19. Odor not distinctive; spore ornamentation only partly covered with amylaceous material 41. *M. mistiformis*

Section **Proto-cystangium** sec. nov.

Peridio in parte exteriore cellulis vesiculosis efformato.

Species typica. *Martellia vesiculosa* S. & S.

21. Martellia **oregonensis** (Zeller) Singer & Smith comb. nov.

Hydnangium oregonense Zeller, Mycologia 33:200. 1941.

Fig. 23.

Gastrocarp 10-20 mm broad, depressed globose, smooth, white, becoming marbled with light and dark brownish spots; gleba white becoming flesh-pink, then brownish-vinaceous, cavities small; columella and sterile base none, odor farinaceous.

Spores 15-18 × 10-15 μ (minus ornamentation), ellipsoid to globose; ornamentation of spines 4-7 × 1.5-2.5 μ amyloid in some manner, either with a thin amylaceous coating over all, with a more heavily amylaceous jacket over lower half and apex nearly hyaline, or upper part even or more irregularly coated with amylaceous material than the lower part; elements closely spaced (but not fused) to somewhat separated; plage area and sterigmal appendage not distinct.

Hymenium continuous. Basidia (30) 35-46(54) × 10-13 μ, clavate, 1-spored, yellowish-hyaline, thin-walled. Cystidia fusoid, scattered to rare, 42-54 × 7-11 μ, thin-walled, hyaline. Basidioles clavate, thin-walled.

Hyphal layers. Subhymenium of inflated cells (sphaerocysts), 2-3 cells deep; mediostratum of interwoven filamentose hyaline thin-walled hyphae 3-6 μ diam. and lacking sphaerocysts; a few subparallel strands forming a rudimentary hymenopodium on each side of mediostratum. Epicutis of peridium a cellular zone 3-6 cells deep, the elements 8-20 μ broad and with thin smooth hyaline walls, from the surface of this layer project numerous small dermatocystidia 15-22 × 4-8 μ, some fusoid ventricose, some clavate, and all with hyaline walls. Context of interwoven hyaline hyphae 3-5 μ diam. and cells scarcely inflated; no sphaerocysts or inflated cells present.

Under duff in mixed woods, Roaring River Fish Hatchery, Linn County, Oregon, April 30, 1938. S. M. Zeller, 8487-type. (NY).

As Zeller pointed out, this is a most interesting fungus. Its unusual characters are the cellular epicutis of the peridium with the small dermatocystidia, lack of sphaerocysts in the context of the peridium, the large spores with their tremendously large spines irregularly coated with amylaceous material, the white color of fresh specimens and the vernal fruiting habit. Zeller 8200, from the above locality on March 20, 1934 is the same. It was identified as *Hydnangium gilkeyae* by Zeller. In it some of the large spines appeared tubular with amylaceous material lining the tubule. Zeller 8459 is a third collection. It was from under incense cedar at Comstock, Oregon, June 15, 1937 and was also identified by Zeller as *Hydnangium gilkeyae*.

22. Martelia **variabilispora** Singer & Smith sp. nov.

Fig. 24.

Carpophoris 15 mm latis, globosis; candidis, gleba alba dein cinnamomeo-ahutecea, loculata; sporis 11-14 × 9.5-12 μ, amyloidesis, subreticulatis. Specimen typicum in Herbarium "NY" conservatum, F. H.

Smith, 4 Oct. 1948, prope "Mary's Peak", Benton County, Oregon, U.S.A.

Gastrocarp 15 mm broad as dried, subglobose, pure white throughout, drying alutaceous; the gleba white at first, drying cinnamon buff; center of gastrocarp cavernous; columella and sterile base none present.

Spores 11-14 × 9.5-12 μ, broadly ellipsoid to subglobose, sterigmal appendage inconspicuous or up to 2.5 μ long, usually with an amyloid basal jacket; ornamentation strongly amyloid, or on larger elements strongly amyloid only at the tip, prominences 0.7-1.5 μ high, in the form of warts and small spines, the elements isolated to grouped into ridges, crescents, or irregular "knotty" short lines (all types usually present on a single spore), very closely arranged but the pale yellowish spore wall visible between elements or groups of elements; plage area not distinctive; hyaline revived in KOH.

Hymenium continuous. Basidia 24-32 × 9-11 μ, 1-spored, clavate, thin-walled, hyaline in KOH. Basidioles numerous. Pseudoparaphyses 10-15 μ broad, clavate, scarcely distinct from basidioles. Cystidia none observed but basidia with sterigma beginning to form remind one of mucronate leptocystidia.

Hyphal layers. Subhymenium cellular and in age the cells enlarged and sphaerocyst-like, hyaline, thin-walled; mediostratum of thin-walled hyaline, smooth, interwoven filaments, not gelatinous in KOH; no sphaerocysts and no oleiferous hyphae present. Epicutis of peridium a cellular layer 4-6 cells deep of hyaline smooth-walled hyphal cells, some clavate end-cells projecting from surface. Context of hyaline interwoven filaments 3-5 μ diam., non-gelatinous and lacking incrustations; no sphaerocysts present and no oleiferous hyphae seen. Clamp connections none.

Under conifers, Mary's Peak, Benton County, Oregon. Coll, Dr. F. H. Smith. October 4, 1948.

This collection was identified by Zeller as *Hydnangium gilkeyae* but the spores readily separate the two, and the epicutis of the peridium is also different. It appears to be related to *Martellia ellipsospora* by spore characters.

23. Martellia **maculata** Singer & Smith sp. nov.

Fig. 26.

Carpophoris 1-2 cm latis, globosis, pallidis, brunescentibus; gleba pallida; sporis 10-15 × 8.5-11 μ, subglobosis, echinatis; aculeolis ad apicem amyloideis; cystidiis nullis. Specimen typicum legit, S. M. Zeller. (*8349*) 6 Nov. 1947, sub "incense cedar", prope Comstock, Oregon, U.S.A. (NY).

Gastrocarp 1-2 cm thick, globose, surface uneven to alveolate, pallid, with brown stains in places; gleba pallid but also with brown stains in places; columella and sterile base absent.

Spores 10-15 × 8.5-11 μ, subglobose to ellipsoid, wall about 1-1.5 μ thick, pale orange to orange buff in Melzer's and nearer cinnamon-buff in KOH; sterigmal appendage inconspicuous; ornamentation in the form of spines up to 1 μ high and 0.5 μ broad which are amyloid only at the tip or on one side near the tip, smaller amyloid granules also present on the spore surface but for the most part all elements unconnected; plage area not different from remainder of surface.

Hymenium. Basidia clavate, 20-24 × 10-12 μ, yellowish in KOH, 2- and 4-spored. Basidioles numerous, content yellowish in KOH. Cystidia none seen.

Hyphal layers. Subhymenium gelatinous, hyaline in KOH, the cells badly collapsed but short and ± isodiametric; mediostratum subgelatinous, hyphae only slightly inflated, hyaline in KOH, thin-walled; no sphaerocysts present. Epicutis an epithelium several cells deep, the walls hyaline to yellowish, smooth, not gelatinous. Context of interwoven hyaline subgelatinous filaments, no sphaerocysts present. Clamps none.

In the Zeller Collections at New York under the name *Hydnangium compactum* Harkness, No. 8349, under incense Cedar, Nov. 6, 1937.

The amyloid reaction of the spore ornamentation is such that the reaction appears spotty under the microscope; some warts show it and some do not, but when present it is clearly evident. The cellular epicutis of the peridium, spore characters and lack of cystidia are distinctive.

24. Martellia **vesiculosa** Singer & Smith sp. nov.
Figs. 27-28.

Carpophoris 1-2 cm latis, globosis, candidis; gleba pallida, loculata; columella nulla; sporis 10-14 × 8-11 μ, echinatis, aculeis integris amyloideis; cystidiis nullis. Specimen typicum legit prope Comstock, Ore. U.S.A. Oct. 20, 1937. S. M. Zeller *8323*, (NY).

Gastrocarp 10-20 mm thick, globose, pure white, gray as preserved in fluid; gleba creamy and unchanging (gray as preserved in fluid) chambers small and irregular; columella and sterile base none evident.

Spores ellipsoid to subglobose 10-14 × 8-11 μ, wall pale yellow in Melzer's and about 1 μ thick; sterigmal appendage short and inconspicuous; plage area not distinctive except for slightly more irregular ornamentation; ornamentation amyloid, of separate rods and warts up to 1.3 μ high, these closely grouped in some areas but not fused, very easily deciduous hence many "glabrous" spores in most mounts.

Hymenium. Basidia short-clavate, 23-28 × 9-12 μ, mostly 2-spored, hyaline, thin-walled, readily collapsing. Basidioles numerous. Cystidia, none present.

Hyphal layers. Subhymenium "cellular" in structure, the cells enlarging to ± 15 μ diam. (sphaerocyst-like); medio-stratum of interwoven hyaline subgelatinous filaments 3-7 μ diam., no sphaerocysts present. Oleiferous hyphae absent. Epicutis of peridium an epithelium of large inflated cells (18-52 μ diam.) with yellowish non-gelatinous smooth walls. Context of narrow (3-5 μ) uninflated non-gelatinous hyphae intricately interwoven and hyphal cells unenlarged; no sphaerocysts present except in subhymenium. Oleiferous hyphae none. Clamp connections none.

In the Zeller collections (NY) under *Hydnangium monticola*, Zeller 8323. Found under incense Cedar, Comstock, Oregon, Oct. 20, 1937. S. M. Zeller.

The tendency for the spines of the spores to slough off in revived material is rather striking. The species is distinguished by the evenly amyloid elements of the spore ornamentation, the fact that the elements are not fused at their bases, and the vesiculose cells of the epicutis.

Section **Martelliella** sec. nov.

Peridio in parte exteriore hyphis filamentosis efformato vel cum pilocystidiis.

Species typica. *Martellia ellipsospora.*

25. Martellia **ellipsospora (Zeller)** Singer & Smith comb. nov.
Hydnangium ellipsosporum Zeller, Mycologia 31:13. 1939.
Figs. 30-31.

Gastrocarp 1-2 cm tall, 1-1.3 cm broad, subglobose, usually taller than broad, smooth but outer layer flaking off in age at times, white to pale ochraceous-buff, occasionally with large white rhizomorphs adhering to surface; gleba cream-color, becoming ochraceous-buff, cavities medium size, "empty"; columella none and no stipe or sterile base present.

Spores 15-20(23) × 12-15(16) μ, broadly ellipsoid, ochraceous in dilute KOH, thin-walled and wall nearly hyaline in Melzer's reagent; sterigmal appendage prominent in some of the smaller spores, usually inconspicuous in larger ones; ornamentation of irregular warts, short ridges and spines and 1.8-2.5(3) × 0.4-1 μ, strongly amyloid or amylaceous material denser over the elements of the ornamentation in some places than in others and usually darkest at or near the apex, sometimes strongly amyloid on one side of a wart and not on the other, the long narrow elements often bent or crooked, *many fine lines* and granules of amylaceous material present and connecting the major elements of the ornamentation; plage area covered with amyloid ornamentation in the form of lines and granules.

Hymenium. Basidia 30-42 × 11-15 μ, mostly 1-spored rarely 2-spored, broadly clavate, thin-walled, hyaline in KOH; those with a sterigmata resembling mucronate cystidia. Cystidia none. Basidioles present, clavate to ellipsoid. Pseudoparaphyses resembling inflated basidioles.

Hyphal layers. Subhymenium cellular, cells sphaerocyst-like and in age quite inflated (10-20 μ); mediostratum a narrow band of interwoven hyaline, branched filaments 4-7 μ in diam., hyphal cells of equal (or nearly so) diameter throughout. Epicutis of peridium as described by Zeller—an outer compactly interwoven layer of narrow hyphal filaments 3-6 μ in diam., the walls thin to slightly thickened but not at all gelatinous. Context of more loosely interwoven hyaline hyphae 5-8 μ in diam., no sphaerocysts found; clamp connections none.

Under conifers, Benton and Clackamas Counties, Oregon, June to August. The type was from under Douglas fir, Alsea Mt. Oregon, June, 1937. Coll. D. P. Rogers. (NY).

By virtue of the giant spores with their peculiar heterogeneous type of ornamentation both as to the amyloid reaction and the shape and size of the elements of the ornamentation themselves, the species is readily distinguished. The lack of sphaerocysts is significant. Zeller's illustration (fig. 19, l.c.) does not show the filamentous structure of the mediostratum as distinctly as Smith observed it on the type, but his indications of its existence are clear. Consequently we have no hesitation in transferring the species to *Martellia.*

26. MARTELLIA **soehneri** (Zeller & Dodge) Singer & Smith comb. nov.
Hydnangium soehneri Zeller & Dodge, Ann. Mo. Bot. bard. 22: 372. 1935.

Fig. 29.

Gastrocarp 6-9 mm diam. globose to reniform, very dark brown to black, surface unpolished; gleba "Sudan brown", cavities relatively large, empty; columella and sterile base none present on specimens examined.

Spores 15-19 × 12-15 μ excluding sterigmal appendage; ellipsoid to subglobose sterigmal appendage 4-7 μ long and with a basal jacket of amyloid material; wall about 1 μ thick and pale ochraceous tawny in KOH, merely hyaline-yellowish in Melzer's; ornamentation amyloid and in the form of rods and warts often fused into irregular short ridges, crescents or octopus-like configurations, isolated small warts and granules also present and frequently these connected by fine lines or merely with "tails", prominences 1-1.5 μ high; plage area not distinctive.

Hymenium. Basidia 1-spored, 42-50 × 9-11 μ, narrowly clavate, wall rigid and pale ochraceous, content when present dark ochraceous to brownish yellow, basidia appearing somewhat staggered in the hymenium, and basidiospores also caught in the layer (basidia growing up around them and these spores eventually covered by walls of old collapsed basidia). Basidioles colored and with walls similar to basidia, often septate 15-20 μ back from apex. Cystidia none.

Hyphal layers. Subhymenium of compactly interwoven broad filamentous much-branched thin-walled hyphae pale ochraceous in KOH and with granular protoplasmic content, darker in color as the dark orange-brown hymenium is approached; mediostratum of interwoven more or less ochraceous filaments with slightly thickened and slightly gelatinous walls, occasional dark rusty brown laticiferous-like hyphae also present. No sphaerocysts present anywhere in tramal plates. Epicutis of pileus basically a turf of compactly arranged crooked, branched hyphae yellow to pale orange-ochraceous in KOH and Melzer's, with some free hyphal ends at surface or these gromped into fascicles. Context of yellowish crooked, subgelatinous hyphae with granular content; conspicuous dark rusty brown laticiferous-like hyphae also present; sphaerocysts absent. Clamp connections absent.

Part of the type studied; Pupplinger Heide bei Wolfratshausen, Führenwald, Bayern, Germany. C. Soehner. (NY).

This is a most incongruous hypogeous species. The large ochraceous (in KOH), ellipsoid spores with their amyloid ornamentation, and the dark orange brown hymenium with imbedded spores are a most unusual set of characters. Actually, as far as we can judge from the material at hand, the hymenium thickens much as one observes it in many of the Clavariae. This, the generally strong tendency to produce ochraceous orange pigment and the subgelatinous tissues as revived in KOH all add to the unusual aspect. The conspicuous deposits of orange-brown wall material in the hymenium are most unusual.

27. Martellia **gilkeyae** (Z. & D.) Singer & Smith comb. nov.
Hydnangium gilkeyae Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 371. 1935.
Fig. 25.

Gastrocarp oblong to subglobose, 45 × 30 × 30 mm, brittle, surface glabrous, with innate reticulate veins, buff with brownish stains, pale tawny when dried and then the wrinkles more pronounced; gleba white becoming slightly creamy when fresh, drying "pinkish-buff" to "warm-buff", cavities open and medium sized; columella and sterile base none.

Spores 12-16 × 12-15 μ (excluding spines), ornamented with prominent simple to forked spines or truncated cones 3.5-5 μ high and 1-2.5 μ broad at base, ornamentation amyloid (denser at apex and around base in many spines), the elements varying greatly in size and not fused at the bases (in fact seldom connected); sterigmal appendage collapsed and inconspicuous; plage area not distinctive.

Hymenium continuous. Basidia 30-37 × 10-14 μ, 1-spored, clavate, thin-walled, hyaline in KOH. Basidioles numerous. Cystidia none but basidia on which the sterigma are developing resemble mucronate leptocystidia morphologically; rarely one sees a pseudocystidial-like filament in the hymenium.

Hyphal layers. Subhymenium of densely ramose-interwoven filaments 3-6 μ in diam., no sphaerocysts present; mediostratum of interwoven narrow (2-4 μ) thin-walled, hyaline non-gelatinous hyphae; no sphaerocysts present. Epicutis of peridium a loose tangled turf of narrow (2-4 μ) clavate to subcylindric hyphal end-cells 12-30 μ long and mostly pale ochraceous and with granular content, much debris adhering in this layer. Context of loosely interwoven hyaline thin-walled smooth non-gelatinous hyphae; sphaerocysts absent; oleiferous hyphae very rare. Clamp connections none.

Hypogeous under *Corylus californicus*, May, Oregon, legit. Helen Gilkey. (Zeller 2334-type). Also April 27, 1935, R. Sprague at Roaring Creek Fish Hatchery.

This species, by its spore characters, is more closely related to *M. oregonensis* than to any other species, but the two differ in the structure of the epicutis of the peridium, in the color of the fresh peridium, and in the cystidia of *M. oregonensis*.

28. Martellia **parksii** Singer & Smith sp. nov.
Fig. 35.

Carpophoris 10 mm latis, globosis, impolitis, rugulosis, cinnamomeo-brunneis (in sicc.); gleba cinnamomea, loculata; columella nulla; sporis 10-14(18) × 9-12(14) μ, echinatis; magis amyloideis in apicibus aculeorumquam in parte inferiore; cystidiis nullis; Specimen typicum legit. prope Comstock, Ore. 6 Nov. 1937, S. M. Zeller *8362* (NY).

Gastrocarp about 10 mm diam. globose, surface uneven to wrinkled and unpolished (when dried out). Near dull cinnamon brown; gleba dull cinnamon-brown, chambers minute; columella and sterile base lacking; consistency rubbery-tough (from material preserved in liquid).

Spores 10-14(18) × 9-12(14) μ, ellipsoid to subglobose, sterigmal appendage 2-3 μ (in addition to above length), with a basal amyloid jacket; ornamentation amyloid and in the form of warts and rods single or in groups but not fused to form distinct lines or ridges, prominences 0.5-1.0 μ high and more heavily amyloid at apex than at base; spore wall merely yellowish in Melzer's sol. about 1 μ thick; plage area not distinct as such; pale buff (about "pinkish-buff") in KOH under microscope.

Hymenium. Basidia 2-spored (only a few with sterigmata seen), 22-28 × 10-13 μ, broadly clavate, thin-walled, readily collapsing. Pseudoparaphyses resembling broad basidioles. Cystidia none found.

Hyphal layers. Subhymenium cellular, the cells 6-10 μ in diam.; mediostratum of interwoven hyaline gelatinous hyphae mostly 2.5-6 μ diam., no sphaerocysts and no oleiferous hyphae in the layer. Epicutis of pileus a turf of minute cells, clavate to filamentous, encrusted with much amorphous material, the clavate cells 4-8 × 3-6 μ and the filaments 4-12 × 1.5-3 μ, various intergrading types present also. Context of narrow (1.5-4 μ) hyaline gelatinous hyphae interwoven and with thin walls; no sphaerocysts present and no oleiferous hyphae. Clamp connections absent.

The type collection was found among those of *Hydnangium parksii* in the Zeller Collections. It is close to the Doty collection of May 31, 1939, but the elements of the epicutis are quite different, the spores are larger, and we doubt if the gastrocarps ever were white.

29. Martellia **californica** Singer & Smith sp. nov.
Fig. 32.

Carpophoris 3 cm latis, irregularibis, impolitis; luteocinnamomeis; columella ramosa; gleba cinnamomea, loculata; sporis 9-12 × 7.5-9 μ, in KOH aurantii-ochraceis, verrucosis, verrucis superne tantum amyloideis; cystidiis 36-52 × 8-13 μ. Specimen typicum legit. prope Guadeloupe, Calif. 9 April 1919, H. E. Parks *521* (NY).

Gastrocarp about 3 cm broad, tuberlike and lobed to irregular in outline, surface unpolished and with much foreign material adhering to it, dull crocens to dull cinnamon; columella apparently dendroid, as judged by streaks of sterile tissue in the gleba; gleba cinnamon, chambered, the chambers small and more or less circular (data all from dried specimen).

Spores 9-12 × 7.5-9 μ, subglobose with a prominent sterigmal appendage, in KOH with an orange-ochraceous content when mature (like the content of the basidia) but when immature hyaline or nearly so, finally thick-walled (0.5-1 μ); ornamentation in the form of low warts 0.25-0.5 μ high and these often amyloid only in upper part, usually separate but on well-ornamented spores some grouped into irregular short lines; plage area not distinct.

Hymenium. Basidia 34-42 × 10-13 μ, 2-, and 4-spored, clavate, hyaline at first but at maturity (sporulating) filled with an orange-ochraceous to orange-brown content. Basidioles hyaline, clavate, thin-walled, 10-15 μ broad. Cystidia scattered (most numerous in cavities near the peridium), fusoid to fusoid-ventricose, 36-52 × 8-13 μ, hyaline in KOH, "empty", thin-walled, originating in the subhymenium (hence of the type known as leptocystidia).

Hyphal layers. Tramal plates with a mediostratum of narrow (3-6 μ) uninflated hyaline hyphae strongly interwoven and subgelatinous in KOH; subhymenium basically of compactly interwoven filaments of very short uninflated cells (but appearing cellular in sections). Epicutis of peridium ochraceous to orange-brown in KOH, basically a turf but elements extremely crooked and interwoven, and the walls often with short out-growths making the layer difficult to dissect, much debris adhering over the surface; context of densely interwoven filaments 3-8 μ diam., the walls slightly thickened and subgelatinous, no incrustations found, no sphaerocysts present. No laticiferous hyphae seen; clamp connections absent.

In forest duff, Guadeloupe, California, April 9, 1919. H. E. Parks, 524. Identified as *Arcangeliella pilosa* by Zeller and then apparently he changed his mind and placed it on the same sheet as *A. cremea*.

This is a most unusual species and one on which adequate color notes would be highly desirable. It differs sharply from *M. cremea* in the highly pigmented basidia and in the ornamentation of the spores, even if one were to discount the epicutis of the peridium. Accurate data on the spore color when fresh are also needed as we believe it will be found to be a valuable species character. The lack of sphaerocysts in the peridium is important also. Since the tissues revive well, the absence of these structures was clearly determined as far as the type specimen is concerned. When this species can be re-described from fresh material in all stages of development, it may be found desirable to erect a genus for it and *M. fallax*.

30. Martellia **fallax** Singer & Smith sp. nov.
Figs. 33-34.

Carpophoris 1-2 cm latis, albidis, brunescentibus; gleba pallide flavida vel pallida; sporis 9-12 × 8-10 μ, subglobosis, in "KOH" luteis; verruculosis; aculeae irregulariter amyloideae; cystidiis 38-50 × 12-17 μ, intus (in "KOH") luteis. Specimen typicum, legit prope Guadeloupe Mines, Calif. H. E. Parks. *Z-253* (NY).

Gastrocarp 1-2 cm in diam., white, turning rusty brown in spots, gleba very pale yellow-cream color to nearly white; odor earthy (notes by Parks).

Spores 9-12 × 8-10 μ, subglobose to globose, sterigmal appendage 2-3 μ long, 1-1.8 μ thick and not amyloid; spore wall up to ± 1 μ thick and yellowish-hyaline in Melzer's sol.; ornamentation in the form of warts and spines 0.5-0.8 μ high and almost as broad, with amyloid material covering the smaller elements but on the larger ones covering only the apex or one side of the wart below the apex, plage area ornamented but the particles there less amyloid and smaller than elsewhere on the spore; spores pale ochraceous to hyaline in KOH.

Hymenium. Basidia 36-44 × 9-11 μ, 2-spored mostly, rarely 4-spored, thin-walled, readily collapsing, many with yellow content in KOH; sterigmata straight and conic. Pseudoparaphyses 10-14 μ broad, ellipsoid. Cystidia 38-50 × 12-17 μ, ventricose-mucronate or apex obtuse, thin-walled, hyaline in KOH or with refractive content as in chrysocystidia.

Hyphal layers. Tramal plates of interwoven, filamentous, subgelatinous hyphae somewhat transparent in KOH, hyaline, with slightly thickened walls, cells uninflated, 4-9 μ diam., no sphaerocysts present; subhymenium of similar hyphae but the cells shorter. Epicutis of peridium of interwoven hyphae hyaline to yellowish in KOH, walls thickened and "glassy" in KOH, surface with scattered dermatocystidia or these present as fascicles; the cystidia subfusoid, 4-8 μ thick and 20-30(40) μ long, hyaline and with walls slightly thickened; context of interwoven filaments; sphaerocysts absent. Clamp connections absent. Laticiferous hyphae absent.

Guadaloupe Mines, Calif., in adobe soil under *Quercus agrifolia*, a thick mat of rotting leaves present, Parkers Z-253. No date given. This was identified as *Arcangeliella socialis* in the Zeller Herbarium.

As a species, the limited extent to which amylaceous material covers the larger elements of the ornamentation is important as is also the lower height of the prominences. But the cystidia are curious. In KOH the hymenium appears yellow from their content and that of the basidia. We do not class the cystidia as "true" chrysocystidia because the same content may also be found in young basidia or even those with sterigmata. These are, rather, leptocystidia in the usual sense but with a colored content. The field characters are practically the same as for *M. ferruginascens*.

31. Martellia **subfulva** Singer & Smith sp. nov.
Fig. 36.

Carpophoris 8-15 mm latis, pallide fulvis, glabris, gleba loculata, cinnamomea; columella nulla; sporis 9-12 × 8-11 μ, pallide cinnamomeis (in "KOH"), amyloideis; cystidiis nullis. Specimen, legit prope Trout Creek, Molalla River, Oregon, U.S.A. 16 June, 1939. Beulah and Helen Gilkey (NY).

Gastrocarp pale rusty brown, 8-15 mm diam. ± globose to irregular, surface glabrous but with some adhering debris; gleba chambered with very fine chambers, dull cinnamon; columella none. Sterile base indistinct in preserved material but a definite point of attachment present.

Spores 9-12 × 8-11 μ, subglobose to globose, pale cinnamon in KOH, wall yellowish in Melzer's; ornamentation strongly amyloid, in the form of rods and spines 0.75-1.5 μ long and 0.3-0.7 μ thick, *more strongly* amyloid at apex than at base, irregular in outline (as focused on from above) or 2-3 fused into an irregular formation but no sign of a reticulum, (the individual groups unconnected but some elements showing fine tails); sterigmal appendage inconspicuous and with a basal amyloid jacket.

Hymenium. Pale cinnamon-yellowish in KOH. Basidia 23-28 × 10-12 μ, clavate, content pale yellowish cinnamon in KOH (preserved material), 2-spored mostly, thin-walled and soon collapsing. Pseudoparaphyses scattered 10-15 μ diam. almost globose at times. Basidioles scattered. Cystidia none found.

Hyphal layers. Subhymenium a layer of large sphaerocysts 2-4 cells deep; mediostratum a narrow layer of filamentose elements hyaline in KOH and not gelatinous, only moderately interwoven. Epicutis of peridium a turf ending in clavate to fusoid cells with ochraceous content, and smaller cylindric to pointed cells with slightly thickened walls. Context

beneath this area ochraceous in KOH and of interwoven narrow hyphae; context near subhymenium nearly hyaline but hyphae also narrow and interwoven; sphaerocysts and oleiferous hyphae none.

In conifer duff along Trout Creek, tributary to Molalla River, Clackamas County, Oregon. 16 June, 1939. Coll. by Beulah and Helen Gilkey.

The above data were from the specimen preserved in fluid. In the dried specimens of the same collection the gastrocarps are dull brown and the gleba dark cinnamon. Revived in KOH the turf forming the epicutis of the peridium is very distinct and the hyphae beneath it rusty brown rather than ochraceous but most of the context shows some ochraceous tone. The spores are pale cinnamon in KOH but strongly amyloid in Melzer's. Also the basidia are more strongly cinnamon in sections from dried material revived in KOH.

This species is most closely related to *Martellia fallax* in color reactions in KOH, the turf of dermatocystidia of the epicutis, and the amyloid spores. It differs in lacking cystidia and in the paler gleba and paler spores in KOH.

32. Martellia **foetens** Singer & Smith sp. nov.
Fig. 37.

Gastrocarpio 30 mm lato, plus minusve globoso; peridio arrhizomorphica, obscure fulvo; gleba loculata, sicca, pallida, cinnamomeo-fuscata ubi laesa, KOH ope flavescente; columella stipiteque nullis. Sporis 9-12 × (7)8-10(10.5) μ, globosis vel subglobosis, pallide ochraceis, spinulis interdum seriatis vel confluentibus superne substantia amylacea obtectis; macrocystidiis paucis nec conspicuis; peridio simplici ex hyphis tangentialibus repentibus prope superficiem brunnescentibus vel fulvescentibus et hyphis nonnullis superficialibus interdum cystidioideis ascententibus formato, plus minusve 150 μ crasso. Specimen typicum legit prope Secesh Summit, Idaho County, Idaho, 10 August 1958. Smith 59864 (MICH).

Gastrocarp 30 mm broad, irregular in outline but roughly globose; peridium glabrous, smooth, without rhizomorphs, dull tawny when collected and drying more or less cinnamon brown; gleba loculate, dry, pallid at first, stained dull cinnamon-brown around worm holes; columella and stipe none (no definite point of attachment); odor when fresh pungent, reminiscent of *Russula foetens;* taste slightly disagreeable.

Spores 8-11 × 7-9 μ, globose or subglobose, ornamentation projecting 1-1.5 μ (rarely 2 μ), spinules 1-1.5 μ broad at base, consisting of heavily amyloid warts and spinules closely spaced and some connected to form chains, others fused into an irregular grouping of ridges or crests but the groups essentially unconnected to other groups, sterigmal appendage often oblique, relatively inconspicuous (2-3 μ long; in dilute KOH the spore pale to dingy ochraceous, the wall typically less than 1 μ thick.

Hymenium. Basidia 27-42 × (6.5)8-12 μ, clavate or nearly so, 4-spored or occasionally 1-, 2-, or 3-spored; sterigmata more often straight than curved, if curved not truly half-sicle-shaped as in agarics, vertical to oblique. Macrocystidia rare to scattered, with banded or granular contents or some hyaline throughout, yellow, becoming blackish in sulfobenzaldehyde, not conspicuously connected with conducting elements (but occasional oleiferous hyphae present in subhymenium or trama), 30-40

× 3.5-8.2 μ, variable in shape, cylindric, clavate, fusoid-ventricose or dumbbell-shaped, smooth and thin-walled.

Hyphal layers. Subhymenium a moderately thick layer of subisodiametric cells 8-15 μ diam. which at times may enlarge considerably to the size and shape of sphaerocystis (20 μ); mediostratum of minflated hyphae 3-6 μ diam. extending in the direction of the tramal plate ("regular"), interwoven, not or only slightly gelatinizing in 2.5 percent KOH. Peridium about 150 μ thick, consisting of a rather uniform layer of tangentially arranged filamentous hyphae which are repent (extending parallel with surface of peridium) but are strongly interwoven, near the surface often strongly colored fulvous brown and with occasional hyphae or cystidioid terminal cells ascending somewhat as in *M. ferruginascens;* the hyphae slightly gelatinous revived in KOH, inamyloid and without clamp connections.

Chemical reactions. KOH causing a yellow stain in the gleba, the pigment dissolving in the medium when mounted on a slide.

Solitary under *Pinus contorta*, Secesh Summit, Idaho County, Idaho, August 10, 1958. Smith-59864-type (MICH).

This species may be easily mistaken for a *Rhizopogon* in the field. The yellow reaction in KOH is an interesting field character, but does not show on revived material. *M. focteus* is close to *M. ferruginascens*, but the odor is distinct, and we believe important, especially in view of the connection to the Russulaceae. In addition there are true sphaerocysts in pockets in the tramal plates of *M. ferruginascens*, i.e., the trama is heteromerous at least to a slight extent.

33. Martellia **brunnescens** Singer & Smith sp. nov.
Fig. 38.

Carpophoris 10-25 mm latis, globosis, albis, glabris, subriticulatis demum alveolatis, brunnescentibus; gleba alba demum brunnea; columella nulla; sporis 8-11 × 8-9 μ, echinulatis, aculeis amyloideis; cystidiis nullis. Specimen typicum, legit prope Roaring River Fish Hatchery, Linn County, Oregon, U.S.A., 31 Mai, 1939; Max Doty (NY).

Gastrocarp 10-25 mm broad, globose or nearly so, white, glabrous, surface uneven to tuberculate and in some specimens finally alveolate, older specimens brownish as if stained; columella and sterile base none; gleba white staining brown, the chambers minute.

Spores 8-11 × 8-9 μ, broadly ellipsoid to subglobose, sterigmal appendage inconspicuous; ornamentation in the form of short spines and warts in groups or evenly distributed but mostly unconnected, the prominences 0.8-1.3 μ high, generally strongly amyloid, especially at apex of the spines; plage area not distinctive or merely with less prominent ornamentation.

Hymenium. Basidia 4-spored and 2-spored, 26-34 × 10-12 μ, clavate, thin-walled, content protoplasmic. Basidioles numerous. Cystidia none.

Hyphal layers. Subhymenium appearing cellular because the hyphae diverging from the mediostratum are cut up by cross walls to produce more or less isodiametric cells; mediostratum of interwoven hyaline gelatinous hyphae 3-5 μ in diam. and *no* sphaerocysts or oleiferous hyphae present in the layer. Epicutis a turf of seta-like dermatocystidia 22-36

× 3-7 μ, fusoid in shape, and walls thin to thickened and yellowish hyaline in KOH, often with patches of amorphous incrustation around them. Context of gelatinous interwoven hyphae 2-4 μ in diameter, hyaline and smooth. No sphaerocysts or oleiferous hyphae present. Clamp connections none.

Type collected at Roaring River Fish Hatchery, Linn County, Oregon, May 31, 1939, Max Doty. Filed under *Hydnangium parksii* in the Zeller Collections (NY).

The above data are all taken from the material preserved in alcohol in the Zeller Herbarium. Apparently none of the material was dried. The distinctive features are the turf of dermatocystidia and amyloid spores with isolated to grouped but unconnected elements of the ornamentation of only moderate height.

A collection by Helen Gilkey at Alsea Mt., Benton County, Oregon, June 2, 1944 was 3 cm in diameter and was identified by Zeller as *H. parksii*. It is the same as the Doty collection, but in it setae resembling the dermatocystidia also occur in the hymenium of the cavities near the context of the peridium. The same brownish stains on the gastrocarp are present in both.

34. Martellia **albella** Singer & Smith, sp. nov.

Carpophoris 10-16 mm latis, subglobosis, albellis, glabris, saepae ochraceo-maculatis; gleba albella, loculata; sporae 11-12 × 9.5-12 μ, subglobsis; cystidiis nullis. Specimen typicum legit prope Puerto Blest, Rio Negro, Argentina, 17 Feb. 1960, R. Singer M-3024 (LIL).

Gastrocarp irregularly globose or potato-shaped, 10-16 mm broad and around 16 mm high, permanently closed and lacking both a stipe and well developed sterile base. Peridium 0.1 mm thick, or a little more (very thin), not breaking up or separable from the gleba when fresh, pallid white, glabrous, smooth, naked, not viscid, sometimes ochraceous spotted in age but not changing color when bruised. Gleba whitish, in age dingy pallid, minutely loculate, tramal plates not lamellate in form but instead irregular and much branched to produce the small chambers which are 0.3-0.7 mm in diameter. Context fleshy, white, unchanging, taste mild, inodorous.

Spores 11-12 × 9.5-12 μ, subglobose, hyaline to pale yellowish; ornamentation projecting 0.7-1.2 μ, of type II (a broken reticulum of coarse crests which are sometimes forked and accompanied by isolatect warts and spines, entirely amylaceous).

Hymenium. Basidia 33-58 × 8-12 μ, hyaline, 2-spored (a few 1-spored), cylindric-clavate to clavate, sterigmata straight to curved. Cystidia and pseudocystidia none seen (sulfobenzaldehyde mounts of freshly dried material showed no brown-black discolorations in hymenial layer).

Hyphal layers: Tramal plates. Hyphae of the mediostratum forming a relatively broad, layer of interwoven filaments or in places subparallel in arrangement, rarely with scattered oleiferous hyphae intermixed, not gelatinized, hyaline; subhymenium variable in thickness and intermittent of intricately interwoven elements with short almost sphaerical cells (up to 10 μ in diam.), all hyaline and from it extend short multiseptate hyphae

extending to the basidia. Peridium consisting of a broad inner layer (the context) and an outer one (the cutis). Both layers of periclinal (appressed) filamentous hyphae, and oleiferous hyphae the latter yellowish and 4-8 μ thick and very numerous in the context; the primordial hyphae mostly yellow and granular on outside (turning brown or fuscous in sulfobenzaldehyde). At the surface the hyphae 3.5-7 μ broad, with rounded tips and occasionally the ends ascendant or erect to form a sparse rudimentary turf. All hyphae lacking clamp connections.

On earth, virtually epigeous, under *Nothofagus dombeyi* Puerto Blest, Rio Negro, Argentina. Feb. 17, 1960, R. Singer M-3024 (LIL), holotypus.

This species is distinguished readily from *M. brunnescens* by the lack of dermatocystidia and by a different pattern of spore ornamentation.

Section Martellia

Epicutis of gastrocarp non-cellular, formed of repent hyphae or a trichodermium of cystidia or hyphal ends.

Type species. *Martellia mistiformis.*

35. Martellia setigera (Zeller) Singer & Smith comb. nov.
Hyduangium setigerum Zeller, Mycologia 31:150. 1939.
Fig. 39.

Gastrocarp 5-15 mm diam., subglobose, attached by a single rhizomorph, surface unpolished to plush-like, white to light brown; gleba creamy white, changing to light brown, cavities small, irregular. Columella and sterile base none.

Spores 8-10(11) μ, globose nearly hyaline as revived in KOH; sterigmal appendage ± 2.5 × 2 μ and with an amyloid jacket around the base; ornamentation in the form of irregular knotty ridges connected to form a broken reticulum and in addition with both small warts and granules with tails, or very fine lines connecting to coarser elements, the prominences about 0.25 μ high (very low), all elements of ornamentation strongly amyloid; spore wall pale yellowish in Melzer's and about 0.5-0.75 μ thick; plage area not differently marked than remainder of surface.

Hymenium. Basidia 30-42 × 10-12 μ, clavate, yellowish as revived in KOH; 1-, 2-, and 4-spored (Zeller), very few seen sporulating in Smith's sections and those seen were 4-spored. Basidioles numerous. Pseudoparaphyses scattered 36-40 × 15-20 μ (resembling giant basidia but none observed bearing sterigmata. Cystidia numerous, 34-52 × 7-11 μ, basically fusoid but near apex usually with a series of constrictions, apices acute, hyaline, content protoplasmic, often seen to connect to oleiferous hyphae; filamentous "pseudocystidia" 30-40 × 3-5 μ and with obtuse apices also present.

Hyphal layers. Subhymenium in the form of diverging hyphae 4-8 μ diam. which are 2-3 septate and in age the cells becoming sphaerocyst-like (up to 15 μ); mediostratum of filamentose-inter-woven hyaline hyphae 4-8 μ in diam. and at junction points some cells barrel-like and up to 12-15 μ broad but no true sphaerocysts present; oleiferous hyphae scattered. Epicutis a trichodermium of thin-walled yellowish to hyaline hyphae with numerous cross-walls and the cells of irregular shape making the layer difficult to interpret, proliferated at the tips into versiform dermatocystidia (10)15-30 × (3)5-8(10) μ, clavate, subfusoid, seta-like or con-

torted-filamentose, if seta-like the cell walls thickened slightly but hyaline in KOH. Context of interwoven narrow (3-4 μ) hyphae with hyaline walls, some barrel-shaped cells scattered through it near subhymenium and a few intercalary sphaerocysts present. Clamp connections none. Oleiferous hyphae present.

Under moss in dense coniferous woods, Roaring River Fish Hatchery, Linn County, Oregon, March 20, 1934. S. M. Zeller 8202-type.

The type was preserved in liquid and this may have affected the color of the setae as these structures were described by Zeller. The above description gives the microscopic data as we obtained them from the type. The species is a *Martellia* even though the spore ornamentation is strongly amyloid. The lack of true sphaerocysts in the mediostratum is the deciding character in this instance. When this species is again encountered, specimens should be dried in the usual manner and sections of such specimens then revived in KOH to get the typical color reactions. We suspect that the basidia in such sections will show a colored content and that the setae may then show as Zeller described them. The structures Smith observed which could be interpreted as endocystidia were oleiferous hyphae.

36. Martellia **monticola** (Hark.) Singer & Smith comb. nov.

Octaviania monticola Harkness, Proc. Calif. Acad. Sci. Bot. III. 1:254. 1899.

Hydnangium monticola (Hark.) Zeller & Dodge, Ann. Mo. Bot. Gard. 22:372. 1935

Fig. 40 and pl. 2, lower figure.

Gastrocarp 10-35 mm broad, globose or nearly so, irregular at times; peridium white but dingy from adhering dirt, at times pinkish-buff in age, outer layer readily separable and often peeled back, much as in *Scleroderma flavidum* Ell. & Ev., inner layer after exposure soon rimose, often so deeply as to expose the gleba; gleba when young, becoming "pale pinkish buff" of slightly paler than "light pinkish cinnamon", loculate, the chambers small; columella a white strip of sterile tissue which branches laterally and is percurrent in some specimens and in others almost lacking, base often with a conspicuous fleshy thickening; odor mild; taste not recorded; context of peridium white and unchanging when cut.

Spores 10-12.5 × 9.5-12 μ, subglobose to globose, hyaline to very pale yellowish in dilute bases; apiculus small and inconspicuous, either straight or oblique; ornamentation in the form of a heavily amyloid broken reticulum with the prominences 0.5-1.1 μ high, rarely with numerous short irregular ridges only partly connected and with isolated warts also present.

Hymenium. Basidia 26-40 × 7.5-12 μ, hyaline, clavate, 2-, or 4-spored, thin-walled and readily collapsing; sterigmata mostly straight, vertical or less frequently oblique. No cystidia of any kind found.

Hyphal layers. Subhymenium broad, consisting of isodiametric cells some enlarged to resemble sphaerocysts, filaments rarely present; mediostratum narrow, consisting of filamentous hyphae relatively frequently septate and somewhat interwoven, lacking sphaerocysts except where tramal plates merge with peridial inner layer; lactiferous hyphae none; oleiferous hyphae occasional. Peridium three layered; with an epicutic-

ular layer consisting mainly of hyphal ends and cystidioid terminal elements not forming a palisade but irregularly ascending and often tangled, the terminal cells cylindric, 24-41 × 4.5-8.5 μ, ampullaceous, subcapitate, clavate, fusoid, etc., apices obtuse to subacute, walls thin to slightly thickened; intermediate layer consisting of tangentially repent filamentous hyphae rarely with slightly swollen cells (to 10 μ diam.), usually 2-4.5 μ broad, hyaline, subparallel to interwoven, not gelatinized, when peridium splits this layer often adheres to the epicuticular layer; inner layer of hyaline heteromerous tissue, sphaerocysts large and abundant; all hyphae inamyloid and lacking clamp connections.

Scattered under *Abies lasiocarpa*.

Material studied. Idaho, Kinney Point, Hell's Canyon, Aug. 20, 1958, coll. T. Westerdale, Smith-60297 (MICH).

This species can be recognized in the field by the manner in which the two outer layers of the peridium split open, giving somewhat the aspect of *Scleroderma flavida*. The spore ornamentation separates it readily from *M. cremea*.

36a. Martellia **alba** (Harkness) Singer & Smith, comb. nov.

Hydnangium album Harkness, Proc. Cal. Acad. Sc. Bot. III, 1.251. 1899.

Gastrocarp about 1 cm thick, subglobose, with a basal point of attachment, pale cinnamon brown and unpolished as preserved in liquid (no dried material); Gleba of small chambers evenly distributed about concolorous with pileus as preserved; no columella or sterile base seen.

Spores globose, 11-13 μ, wall yellowish in Melzer's and pale buff in KOH, 1-1.5 μ thick; ornamentation in the form of chains of warts connected by fine lines to produce a broken reticulum, or the warts grouped into short ridges very irregular in outline and with fine lines radiating but not connected to form a reticulum, isolated warts few, when present typically with tails, prominences 0.4-0.8 (1 μ) high (mostly relatively low ornamentation); sterigmal appendage short, inconspicuous, centrally attached; plage area not distinguishable.

Hymenium continuous, basidia 1- 2-spored, 30-40 × 10-15 μ, clavate, hyaline in KOH (isolated), thin-walled and readily collapsing. Pleurocystidia 20-40 × 10-13 μ, cylindric to clavate or tapered to a blunt apex, content evenly highly refractive (not granulose), scattered to rare, imbedded in the hymenium and also present as endocystidia in subhymenium and trama.

Hyphal layers. Subhymenium of interwoven filaments 5-9 μ, giving rise to inflated cells near base of basidium and these 10-15 μ diam. Mediostratum of interwoven hyphae with enlarged hyphal cells up to 15 μ diam., and scattered laticiferous or oleiferous hyphae with refractive granular content, 5-12 μ in diam., groups of inflated cells sometimes present at junctions of tramal plates and where plates join the peridium. Peridium of a thick (100 μ +) layer of hyaline hypha 2-4(6) μ in diam. appearing near the outer surface to be loosely interwoven and somewhat "glassy" in KOH as though gelatinous originally, this layer extending

to the subhymenium but more compactly interwoven inward. Clamp connections none.

In the forest, California, spring.

Through the courtesy of Dr. Ira Wiggins, at the Dudley Herbarium, Stanford, University. Smith has been able to examine the "co-type," which, as we read the number on it, reads 174 instead of 178, but the numeral following the 7 is not too clear. Smith's data do not check well with that given by Zeller and Dodge (1936) as to dark brown bodies resembling latex organs, and the short sharp spines of the spores, and the basidia which they give as 20 × 6 μ. Our measurements are based on basidia with sterigmata, but the sterigmata are not included in the measurements. The hyphae of the mediostratum are "physalomitic," and if one interprets the largest elements as sphaerocysts then these may be said to be scattered. In this character the layer resembles that forming the interior context in the peridium of *M. mistiformis* and a close relationship to that species is not at all improbable. It would appear however, that in *M. alba* the inner (context) layer of the peridium was so reduced as to be evident only in areas where the tramal plates meet the peridium. Although we place this species in *Martellia* we recognize it as one which is borderline and could with some justification be referred to *Gymnomyces*.

37. Martellia **occidentalis** Singer & Smith sp. nov.
Fig. 41.

Carpophoris circa 1 cm latis, subglobosis, in siccati atro reticulatis, duris; columella percurrente; gleba loculata, avellanea; sporis 11-14(17) × 10-13(15) μ, tenuicatis, globosis; subspinulosis, aculeis amyloideis. Specimen typicum, legit prope Saratoga, Calif. 23 March, 1919. J. McMurphy *272* (NY).

Gastrocarp up; to 1 cm diam. subglobose; peridium blackish, wrinkled and hard; columella percurrent as a blackish line of sterile tissue; gleba of chambers about 0.5 mm in diam. round or nearly so and filled with "avellaneous" material (spores). Above data taken from dried specimen.

Spores 11-14(17) × 10-13(15) μ, globose to subglobose, wall thin, many spores remaining collapsed in Melzer's reagent, ornamented with warts and spines 1-1.5(2) × 1 μ, ornamentation *strongly* amyloid, elements closely arranged but mostly separate (2-3 fused on some spores in places), spaces between the elements non-amyloid, spore in KOH yellowish-hyaline; sterigmal appendage inconspicuous and lacking any coating of amylaceous material.

Hymenium. Basidia 4-spored, 36-44 × 10-17 μ, clavate, sterigmata very fine, conic, about 4 × 1 μ. Pseudoparaphyses 30-36 × 16-24 μ almost ellipsoid, thin-walled, hyaline (in KOH). Cystidia none.

Hyphal layers. Tramal plates of interwoven "glassy" hyphae in KOH, about 5-6 μ in diam. and with hyaline walls, no sphaerocysts or laticiferous hyphae seen; subhymenium of cellular elements at times considerably enlarged (sphaerocysts). Epicutis of pileus a thick gelatinous layer about 200 μ thick or more and with slightly less gelatinous tissue forming the body of the context, all hyaline in KOH and yellowish hyaline in Melzer's reagent. Sphaerocysts rare and mostly near the subhymenium of the outer glebal cavities. Clamp connections none. Laticiferous hyphae rare.

Under oak, Saratoga, Calif. Coll. J. McMurphy, No. 272. March 23, 1919. Identified as *Arcangeliella occidentalis* in the Zeller Herbarium.

The name *Octaviania occidentalis* should perhaps be discarded as a nomen confusum. Harkness in his original account did not mention a latex, and if we interpret his language correctly, the gastrocarps have a sterile base from which branches of sterile tissue extended into the gleba as a dendroid columella. We quote: "Large, 2.5 cm in diam. color white, turning brown, semiglobose; common integument flakey; absorbent base firm, terminating in branching fibrillae; gleba cells white; cells oblong or subrotund, basidia 4-spored; spores briefly stipitate, white, globose, echinulate, having about twenty blunt projections on the circumference 14 μ diam." Whether one interprets the statement about the sterile base as we do or as terminating downward and there giving rise to fibrils, it is evident that Harkness did not say anything about a percurrent columella. These two characters Zeller and Dodge must have obtained from the cotype, and this causes us to wonder if the original collection was a mixture of species.

In any event, the species Harkness described and the one McMurphy collected (as No. 272) are two different fungi. The outstanding features of the McMurphy collection are the broad basidia (10-17 μ) the absence of cystidia, and very likely the presence of gelatinous tramal tissues. The McMurphy collection, in addition had filled glebal chambers, but the importance or meaning of this character needs further study.

38. Martellia **idahoensis** Singer & Smith sp. nov.
Figs. 42, 45-46 and pl. 2, center figure.

Gastrocarpio 8-40 mm lato, globoso-depresso vel irregulari; peridio cristulis irregularibus ornato, albo, duplici; gleba alba, demum cinnamomeo-alutacea minute loculata, sicca; columella a basi sterili exigua dendroidee extensa, lineari, manifeste percurrente, in siccis facile praetervisa; carne alba, immutabili. Sporis 10.5-13 × 9.5-11.5 μ, globosis vel breviter ellipsoideis, aculeis longis echinatis iodi ope typi VI modo ornamentatis, partim amyloideis. Basidiis 2-4-sporis. Cystidiis pseudocystidiisque praesentibus. Peridio in parte interiore hyphoso ex hyphis filamentosis composito (parte interiore plus minusve 350 μ crassa); in parte exteriore (200 μ lata) e catenulis hypharum pancarum filamentosarum numerosissimorumque elementorum inflatorum sphaerocystiforminm (e. gr. 26 × 15 μ) efformato, membris terminalibus catenularum hyphiformibus, clavatis (e. gr. 40 × 10 μ), irregularibus rarius cystidiformibus, ex toto haud gelatinoso. Specimen typicum, legit prope Squaw Meadows, Idaho County, Idaho, Aug. 1958, Smith *60161* (MICH.)

Gastrocarp 8-40(50) mm broad, globose- depressed, circular or quite irregular in outline; peridium uneven to ribbed with irregular ridges and grooves, more or less distinctly radiating from the base of the carpophore (point of attachment), at first merely wrinkled, with little or no dirt adhering to the surface, white to dead white when young, finally with a pale alutaceous tone in some areas, rarely over all, drying pallid, two-layered, the outer layer separable, thin (little more than half a millimeter thick when dried); gleba white, in age pale cinnamon buff, composed of minute, irregular empty chambers, dry in consistency when cut;

columella poorly developed, dendroid, in fresh material observable as a few white lines of sterile tissue extending out from a small basal tubercle of sterile tissue or a thickened basal portion of the interior layer of the peridium. Context of peridium white, unchanging, odor none, taste not recorded.

Spores 10-13 × 9-11.5 μ, globose to broadly ellipsoid; sterigmal appendage very inconspicuous, straight or oblique, attached at geometric base of spore; ornamentation essentially echinate to verrucose, the prominences 1-1.5(-2) μ high, elements unconnected or anastomosing to form compound warts which are also more or less unconnected to each other, very few anastomosing lines or ridges, amylaceous material denser at apex of the spines and warts.

Hymenium. Basidia 29-45 × 11-16 μ, clavate, hyaline, (1-), 2-, 3-, and 4-spored; sterigmata 5-8 μ long, narrowly conic, erect or slightly oblique, straight or nearly so, apical. Macrocystidia arising from deeper in the tramal tissue than the basidia, 40-50 × 9-10 μ, with banded to granular pale yellowish content turning brown in sulfobenzaldehyde, clavate to subcylindric, obtuse, scattered. Leptocystidia (?) rare, 30-37 × 12-15 μ, clavate-mucronate and with weakly refractive amorphous interior mass as revived in KOH; a second type (76-90 × 9-14 μ) present and narrowly clavate, found on fresh material but not demonstrated again from dried material, their content hyaline and homogeneous and the wall very slightly thickened.

Hyphal layers. Subhymenium broad, cellular, of large and small sphaerocysts; mediostratum of tramal plates relatively narrow, composed entirely of filamentous hyaline subparallel to silghtly interwoven hyphae extending in the direction of the tramal plates; laticiferous hyphae rare (best seen in immature fruits), brown in KOH, crooked. Peridium consisting of an epicuticular layer over 200 μ thick consisting of a staggard palisade of hyphae with enlarged cells and ending in clavate end-cells, or these showing irregular proliferations, rarely with narrow or branched elements in the palisade; interior to this layer is a layer of repent filamentose hyphae more or less interwoven and with pockets of slightly inflated cells (rudimentary sphaeroeysts), not at all gelatinized. Clamp connections absent; all hyphae inamyloid.

Chemical characters. $FeSO_4$, KOH and ethyl alcohol not showing any color reaction in or on the peridium or gleba.

Solitary to gregarious, beneath the duff under *Picea englemanii* and *Abies lasiocarpa*, common in the type locality.

Material studied. Idaho, Squaw Meadows, Valley County, Idaho, August 1958, Smith-60161, type (MICH); additional collections Smith-60260, 60272, 60361, 60363, 60367, 60597, (all paratypes, MICH).

This species, which grows along with *Gymnomyces ferruginascens*, can be distinguished from the latter by its clean wrinkled appearance. It does not become brown from handling. The leptocystidia are rare and neither of us has been able to demonstrate them on the dried material. It is clear to us that the only readily demonstrable type of cystidia in the hymenium is the macrocystidial type. Balloon-shaped pseudoparaphyses can be found here and there in the hymenium.

39. Martellia **scissilis** (Zeller & Dodge) Singer & Smith comb. nov.
Arcangeliella scissilis Zeller & Dodge, Ann. Mo. Bot. Gard. 22:369. 1935.
Fig. 47.

Gastrocarp up to 3 cm broad, surface very smooth, yellowish drying tawny; columella thin, white, extending about half way to apex; gleba creamy, drying antimony-yellow, compact; odor strong of witch-hazel.

Spores 10-14 μ (minus ornamentation), globose to subglobose; sterigmal appendage prominent, 4-5 μ long; ornamentation in the form of fine spines and rods 0.7-1 × 0.5 μ which are amyloid only at the tips and are not connected to each other; the spore wall between the spines non-amyloid.

Hymenium. Basidia 4-spored, 20-25 × 8-11 μ, short-clavate, thin-walled, sterigmata 3-4 × 1 μ, short-conic; basidioles 15-23 × 8-10 μ, clavate, thin-walled. Pseudoparaphyses none. Cystidia abundant, 40-55 × 9-16 μ, obventricose-mucronate, thin-walled, readily collapsing, smooth, content hyaline and homogeneous (leptocystidia).

Hyphal layers. Subhymenium of cellular structure. Mediostratum of tramal plates interwoven, hyaline and with hyphae having walls 0.5-0.7 μ thick, glassy in KOH, no sphaerocysts demonstrated. Peridium a thick hard (as dried) layer of interwoven hyphae with "glassy" walls in KOH. Epicutis not differentiated but surface hyphae with ochraceous to brownish walls and apparently a sparse covering of narrowly clavate hyphal end-cells forming a sparse turf. Innermost layer apparently with scattered sphaerocysts (vesiculose "holes" seen in this area). Oleiferous hyphae rare. Clamp connections none.

Under conifers, Northern California, November. Material studied: H. E. Parks No. 4125.

The hard peridium, the difficulty in macerating the sections and the refractive character of the hyphae in the peridial wall are distinctive features. The almost pseudoamyloid spores with the slight amyloid reaction at the tips of the spines forming the ornamentation are also important characters. On the basis of such characters as these in addition to the odor of witch-hazel, there should be no difficulty in recognizing the species.

40. Martellia **cremea** (Zeller & Dodge) Singer & Smith comb. nov.
Arcangeliella cremea Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 367. 1935.
Figs. 43-44.

Gastrocarps 10 × 20 × 20 mm, irregular in shape, drying subreniform, light buff to cinnamon-buff, marbled; columella precurrent, creamy white; gleba firm, cinnamon-buff. The type is pallid yellowish as dried.

Spores globose to broadly ellipsoid, 10-12(14) × 9-12 μ, (without ornamentation), ornamentation of strongly amyloid, isolated spines closely set and generally of two sizes: 1) 1.2-2 μ high and 1.5-2 μ at base, conic; and 2) smaller warts or amyloid particles 0.5-1 μ in diam. and about as high, no connecting lines seen, the tips of the spines often with an amyloid plug, over the plage area of the spore usually a few fine amyloid lines present and connected to form a partial reticulum and the warts and

spines on that area greatly reduced in size, the ornamentation easily broken off and littering the mount.

Hymenium. Basidia 26-33 × 8-12 μ, 2- and 4-spored, clavate, hyaline, thin-walled, sterigmata 6-8 × 1.5 μ, conic and narrow; pseudoparaphyses subelliptic, 10-16 μ in diam., thin-walled; cystidia scattered, 35-46 × 12-17 μ, ventricose-mucronate, rarely with refractive, amorphous content (but when present not same type as in chrysocystidia), mostly remaining collapsed.

Hyphal layers. Hyphae of tramal plates interwoven, hyaline; subhymenium of sphaerocysts-like cells. Peridium with a thick (about 100 μ) outer filamentose epicutis of hyphae 3-5 μ in diam., hyaline interwoven, and not incrusted, inner layer heteromerous; clamp connections none. Oleiferous hyphae rare to scattered.

In duff, under oaks, Oregon, March. Zeller 7927-Type.

The distinctive features of the species are the mucronate cystidia and the great variability in the height of the spore ornamentation. The lack of a cellular outer (epicuticular) layer in the peridium and lack of a stipe-columella are all that keep this species out of *Cystangium*. The spines on the spores are covered with amylaceous material but the deposit is thicker near the spine-apex.

41. Martellia mistiformis Mattirolo, Malphigia 14:78. 1900.
Hydnangium mistiforme (Mattirolo) Zeller & Dodge, Ann. Miss. Bot. Gard. 22:372. 1935.

Gastorearp about 10 mm thick, subglobose, sterile base rudimentary; peridium smooth, easly separable from the gleba, variable in thickness, whitish olive; gleba lacmose, chambers small irregular, gyrose, irregularly arranged but tending to arise in rows mostly from the base (but not lamellate), color umber to chestnut, the tramal plates cottony-filamentous and often scissile at junctions.

Spores 11-13.5 × 9.5-12.5 μ varying from hyaline to brown, pigment localized in the wall when present, wall thin or up to 1.5 μ thick: ornamentation 0.7-1.5 μ high, hyaline to brownish hyaline (NH_4OH and KOH), consisting of a fundamental ornamentation of narrowly conic spines which are isolated (type VI), surface typically only partly covered with amylaceous material—only at the tip, or on one side, etc.; sterigmal appendage centrally or eccentrically attached.

Hymenium. Basidia 4-spored, sterigmata straight and conic, erect or oblique. Cystidia not demonstrated conclusively (one brown, somewhat projecting and deeper rooting element seen as well as one which was hyaline and mucronate).

Hyphal layers. Subhymenium very broad, cellular, consisting of voluminous sphaerocysts; mediostratum narrow to very narrow, distinctly regular and dense, not gelatinized. Peridium consisting of two layers, the epicutis very densely compacted of hyphae about 2 μ thick, hyaline and mainly tangentially arranged but strongly interwoven, in some areas irregular in shape; context hyaline and similar to epicutis in structure but hyphae broader and even more strongly interlaced, with some very short and broad elements scattered through it but not typically heter-

omerons since the shorter elements are not like the sphaerocysts of the subhymenium, they are smaller and irregular in shape. All hyphae inamyloid and lacking clamp connections.

Subhypogeous or hypogeous under sugar oak (Quercie de Sughero), May. Italy. Sardinia, Orune, leg. U. Martelli, type (F. H. Patouillard Herbarium).

Zeller and Dodge state that the peridium is composed of jellified compact hyphae, but the peridial tissue as observed on the type showed no tendency toward gelatinization even when subjected to pressure in warm 10% KOH. Either there was once a gelatinous outer layer which has been obliterated or, more probably, there never was such a layer over the peridium. Zeller & Dodge described the spores as umber and slightly echinate.

GYMNOMYCES Massee & Rodway

Bull. Miscel. Infor. Kew p. 125. 1898.

"Peridium haud distinctum vel nullum. Gleba carnosa, ad basin fertilis, extus intusque lacunosa, cellulis cavis ubique subaequalibus; septa haud scissilia. Basidia pleurumque 2-spora. Sporae globosae, hyalinae, echinulatae vel verrucosae."

Differs from *Gautieria* in the hyaline globose spores. Some species of *Octaviania*, in which the peridium is very delicate, bear some resemblance to the species included in the present genus, but are distinguished by the well developed sterile base and the tinted spores."

For our own interpretation and definition of this genus see *G. pallidus*.

Type species. *Gymnomyces pallidus* Massee & Rodway. l.c.

KEY TO SPECIES

1. Peridium white, becoming rose-tinted; spores with a heavy amyloid deposit at the base of or partly surrounding the sterigmal appendage . . . 43. *G. roseomaculatus*
1. Not as above . . . 2
2. Basidia ochraceous tawny as revived in KOH . . . 44. *G. cinnamoneus*
2. Basidia hyaline or nearly so in KOH . . . 3
3. Spores with inamyloid spines and a low broken amyloid reticulum between them; gastrocarp with evanescent peridium . . . 45. *G. alveolatus*
3. Not as above . . . 4
4. Spores 7-9(11) × 6-8 μ, ornamentation in the form of a broken reticulum, the prominences 0.25-0.4 μ high . . . 42. *G. pallidus*
4. Not as above . . . 5
5. Epicutis of appressed, interwoven hyphae (scattered dermatocystidia may be present over surface) . . . 6
5. Epicutis in the form of a distinct trichodermium . . . 7
6. Columella present and percurrent; gleba rose pink when fresh . . . 46. *G. socialis*
6. Columella none; gleba white at first . . . 47. *G. compactus*
7. spores 12-14(18) × 9-12(15) μ; gastrocarp white changing to brown . . . 48. *G. ferruginascens*
7. Spores 8-11 × 7-9 μ; gastrocarp white and unchanging . . . 49. *G. parksii*

42. GYMNOMYCES PALLIDUS Massee & Rodway, Bull. Misc. Inf. Kew p. 125. 1898.

Fig. 48.

"Gleba globosa, irregularis, initio albida, dein sordida, cellulis majusculis irregularibus, sordide albidis; septa tenuia, albida, nec scissilia.

Sporeae globosae, 9-10 μ diam., hyalinae, verruculosae, saepe brevissime caudatae, in quoque basidio binae, sterigmatibus brevibus suffulatae."

"Underground, Rodway 299."

"Irregularly spherical, 2-4 cm in diameter, very fragile, no distinct peridium. Sterile base obsolete but in one specimen growing into a slender stem emerging from an umbilicus."

The original data are quoted above for the genus and the type species. We have studied Rodway 1277 marked Co-type in the Zeller Herbarium and obtained the following data.

Spores 7-9(11) × 6-8 μ, broadly ellipsoid to subglobose, ornamented, the ornamentation in the form of a broken reticulum, the elements 0.25-0.4 μ high and very "knotty" in appearance and coated with a strongly amylaceous material; spore wall thin; sterigmal appendage short and pointed.

Hymenium. Basidia 4-spored, clavate, 26-30 × 8-9 μ, hyaline in KOH and readily collapsing. Cystidia scattered to abundant, 30-40 × 5-8 μ, subcylindric-mucronate and with some hyaline refractive amorphous material in the interior, thin-walled, not encrusted.

Hyphal layers. Subhymenium of inflated cells but these not much broader than the diameter of the basidioles (not true sphaerocysts); hyphae of tramal plates interwoven and with occasional sphaerocysts, hyaline in KOH. Peridium with an outer layer (epicutis) of gelatinous interwoven hyphae 3-6 μ in diameter, hyaline in KOH or yellowish only at the surface; interior to the epicutis is a thin layer showing some sphaerocysts, hyaline in KOH; laticiferous hyphae present. Clamp connections absent.

In order to clearly establish the position of this genus the holotype must be studied. "Co-type" material showed an obvious peridium and 4-spored basidia. *G. pallidus* was placed in synonymy with "*Areangeliella alveolata*" by Zeller & Dodge very likely on the basis of Rodway's collection 1277. This collection (designated packet 3 in the Zeller collections under the above name) is specifically different from the numerous other species found under that heading in the Zeller Herbarium.

The following is an account of our study of the material filed under the name *A. alveolata* in the Zeller Herbarium. The packets have now been numbered 1-7 and are reported on here in that order.

Packet 1. From under mixed shrubs near Peoria, Linn County, Oregon, coll. and det. S. M. Zeller, Oct. 1922. Part of one gastrocarp present. Spores 9-11 × 7-9(10) μ, globose to subglobose, ornamented by ridges and lines of granules coated with amylaceous material, the heavy lines extending clear around the spore and often approximately radiating from near the sterigmal appendage; wall between elements of ornamentation hyaline in Melzer's reagent; ornamentation about 0.5-1 μ high for heavy lines 0.25 μ for finer lines and particles.

Basidia 4-spored, 40-55 × 9-12 μ, narrowly clavate, sterigmata conic, straight, 5-6 × 1.5 μ; basidioles numerous; cystidia absent or possibly as ends of laticiferous hyphae merely projecting into the hymenium (these demonstrated on crushed material). Tramal plates with mediostratum of heteromerous tissue; subhymenium of isodiametric cells about as broad

as the base of the basidia. Peridium with a thick outer layer of subgelatinous hyphae in KOH, 5-9 μ in diam., interwoven, and interspersed are many laticiferous hyphae, inner layer apparently with some sphaerocysts. Clamp connections none.

Conclusion. The spore characters alone clearly indicate that this material is not the same as Rodway 1277. See notes on packet 4.

Packet 2. Under Oak, Berkeley, Calif. coll. N. L. Gardner, Nov. 24, 1904. Spores 7-9(11) μ, globose to subglobose with an inconspicuous sterigmal appendage; ornamentation in the form of long ridges extending more than half way to entirely around the spore, some shorter ridges and granules present between the heavier ones, the heavy ones 0.25-0.5 μ high. Basidia 36-45 × 7-9 μ, ventricose below the apex, 4-spored; sterigmata conic, many curved, 4-5 × 2 μ (at base). Basidioles abundant. Cystidia none.

Subhymenium cellular, the cells the same diameter as the base of the basidioles but about isodiametric (no true sphaerocysts present); tissue of the trama plates heteromerous, filaments interwoven, hyaline in KOH and yellowish in Melzer's reagent. Laticiferous hyphae present. Peridium of interwoven hyaline hyphae 3-8 μ in diameter, no differentiation into an outer layer, subgelatinous in KOH; laticiferous hyphae present; sphaerocysts absent; clamp connections absent.

Conclusion. This material appears to be the same species as that in packet 1, though the ornamentation of the spores is slightly lower and the peridium as observed shows more reduction.

Packet 3. This is Rodway No. 1277, already described in this account.

Packet 4. L. Rodway No. 1280, from Cascades; "co-type" material of *Hydnangium glabrum*. (Fig. 49.) This material is the same as that in packet 1. No new combination is proposed because of the very real possibility that the holotype is different than Rodway 1280.

Packet 5. H. C. Parks 477 (Z-27). This is *G. parksii*, see that species.

Packet 6. Gardner No. 220. See *Macowanites gardneri* S. & S.

Packet 7. See *Gymnomyces cinnamomeus*.

Discussion. It is evident from an examination of the seven packets that "*Areangeliella alveolata*" must be redescribed from an examination of the holotype in order to clarify and properly define its limits. There is nothing in the original account to indicate that *G. pallidus*, or the genus *Gymnomyces*, for that matter, is characterized by the presence of a latex. Thus we believe the genus belongs in the *Russula* series of the Astrogastraceae where the thin apparently transparent peridium, or the absence of a peridium, would be its chief claim to distinction, and it should be remembered that the reduced peridium was precisely the character emphasized by Massee and Rodway when they erected the genus. On the basis of the present data we would arrange the genus along with *Martellia* at a lower level than those with a well differentiated stipe-columella such as *Macowanites*. We have extended the concept of *Gymnomyces* here to include species with a well defined peridium, rather than describe a new genus. However, if it should be found that in the holotype of *G. pallidus* the mediostratum of the tramal plates does not contain sphaerocysts, then a new genus would be in order.

Revised description of Genus. Gastrocarp globose to subglobose; peridium varying from thin and evanescent to well-formed, the inner layer when more than one is present often containing sphaerocysts; gleba chambered, cavities empty or nearly so, tramal plates in sections showing at least scattered sphaerocysts; columella present or absent but not in the form of a percurrent stipe-columella. Spores ornamented and the ornamentation amyloid to partly amyloid.

43. Gymnomyces **roseomaculatus** Singer & Smith sp. nov.
Fig. 50.

Carpophoris 1-5 cm latis, globosis vel irregulare, rimosis, albis, dein roseo-maculatis; gleba alba demum alutacea; columella nulla; sporis 14-17 × 12-16 μ, subglobosis vel breviter ellipsoideis, echinatus ("Type VI, Singer system"); cystidiis 43-62 × 12-18 μ, hyalinis vel intus ochraceo-fulvis. Specimen typicum legit prope Saratoga, Santa Cruz Mts., California, (NY). U.S.A. March, 1919, H. E. Parks Z-19.

Gastrocarp 1-5 cm in diam, very irregular in shape, with a tendency to split or crack when mature; peridium thin but persistent, white but tinged or spotted with rose or bright red, gradually discoloring to brownish over all; gleba white, turning tan, chambers very small but not filled; columella none evident (Parks made no mention of it); odor very penetrating, resembling that of witch-hazel.

Spores 14-17 × 12-16 μ, subglobose to broadly ellipsoid, with a sterigmal appendage 3-4 × 2-3 μ, ornamentation in the form of closely set rods 1-1.5 × 0.6-1 μ, *not* fused even though bases may touch, strongly amyloid, *typically with a large mass of amyloid material to one side of or partly around the sterigmal appendage*, spore-wall thin and nearly hyaline in Melzer's reagent, yellowish-hyaline to pale dingy orange-ochraceous in KOH.

Hymenium. Basidia 30-35 × 12-14 μ, clavate, 2-spored, readily collapsing; pseudoparaphyses present, 25-30 × 15-20 μ; cystidia 43-62 × 12-18 μ, ventricose-pedicellate, tapered evenly, also tapered to an obtuse or subacute apex, thin-walled, either empty (hyaline) or with golden ochraceous somewhat granular content in KOH (but not typical of chrysocystidia), walls thin and smooth.

Hyphal layers. Tramal plates of broad filaments and some sphaerocyst-like cells, filaments interwoven, pallid yellowish to hyaline in KOH; subhymenium of sphaerocyst-like cells 1-3 deep, hyaline, thin-walled. Epicutis of peridium of interwoven hyphae but some free ends present, hyphae 4-10 μ diam. and ochraceous in mass (in KOH), much debris adhering along hyphae in and over this layer; context heteromerous but sphaerocysts not abundant, filaments loosely arranged, clamp connections none; laticiferous hyphae very rare.

In an open field under grass near *Quercus*, Saratoga, Santa Cruz Mts., California. March 1919. H. E. Parks Z-19, type.

This species has more than its share of distinctive characters. The white peridium which develops rose colored spots or areas coupled with the pungent odor of witch-hazel should be a valuable combination of field characters. Under the microscope the heavy mass of amyloid material

beside or partially surrounding the sterigmal appendage is unusual, and in addition to this we have the large cystidia with their golden subgranular content in KOH.

44. Gymnomyces **cinnamomeus** Singer & Smith sp. nov.
Figs. 51-53.

Gastrocarpio 10-25 mm lato, subgloboso, glabro, in siccis cinnamomeibrunneo; gleba cinnamonei-brunnea, loculata; sporis 9-12 μ, globosis, praecipue in parte superiore aculeolorum amyloideis, echinatis; basidia in "KOH" ochraceo fulvis; cystidii nullis. Specimen typicum, legit prope Berkeley, Calif. 7 January 1905, N. L. Gardner (NY).

Gastrocarps as dried globose to subglobose, 10-25 mm broad, surface glabrous, cinnamon-brown; gleba chambered, pale cinnamon-brown, no columella showing; point of attachment not definite.

Spores 9-12 μ not including the sterigmal appendage, globose to subglobose, ornamentation amyloid and consisting of short spines up to 1 μ high and warts, the amyloid reaction limited mostly to the upper half of the spines and warts, some weakly amyloid ridges and connecting lines also present and often forming half crests or half circles; sterigmal appendage oblique and projecting about 3 μ, pointed.

Hymenium. Basidia 4-spored, 38-55 × 10-13 μ, clavate, readily collapsing, *ochraceous to tawny* as revived in KOH, sterigmata irregular in size 4-7 or 11 μ long on the same basidium, sometimes conic. Cystidia none found (hymenium revived fairly well). Pseudoparaphyses present, clavate to vesiculose.

Hyphal layers. Mediostratum of tramal plate heteromerous and some oleiferous hyphae present, subhymenium cellular, cells about same diameter as base of basidium. Peridium with a thick outer layer of narrow interwoven subgelatinous hyaline filaments 3-10 μ diam., sphaerocysts present in a thin poorly defined inner layer. Clamp connections none.

Hypogeous under *Quercus agrifolia*, Univ. of Calif. campus, Berkeley, Calif. Jan. 7, 1905, coll. N. L. Gardner.

Material studied. The collection designated as packet number 7 in the *Arcangeliella alveolata* collections of the Zeller Herbarium.

The spore ornamentation varies from true broad cones to crests or half-circles and some spores predominantly show the latter. As dried the specimens remind one of *Martellia foetens* and *G. ferruginascens* but the latter two definitely occur under conifers and the ornamentation of the spores appears to distinguish them further. The colored basidia in KOH also appear distinctive.

45. Gymnomyces **alveolatus** Singer & Smith sp. nov.
Figs. 54-56.

Gastrocarpio 3-5 cm lato, subgloboso; peridio papyraceo demum evanescente; gleba loculata; alutacea; columella tenui; sporis 9-12 μ, globosis, aculeolis in-amyloideis sed reticulatione basali partim amyloidea; cystidiis 30-37 × 4-8 μ, filamentosis vel subbrentricosis, curvulis. Specimen typicum, legit prope Corvallis, Oregon, 23 May 1929. S. M. Zeller *6862* (NY).

Gastrocarps 3-5 cm thick, globose to irregular in outline, pale dull ochraceous tawny as dried, with an inconspicuous basal attachment, (al-

most like a thick rhizomorph); peridium thin and at maturity evanescent, the glebal chambers showing as an alveolate pattern on outer surface; gleba chambered, chambers empty, color "cinnamon-buff" as dried; columella slight, as a few thin lines of sterile tissue penetrating through gleba to the surface, sterile base small and inconspicuous.

Spores 9-12 μ, globose; sterigmal appendage inconspicuous, non-amyloid; wall thin (0.5 μ) and pallid yellowish in Melzer's reagent, nearly hyaline in KOH; ornamentation of scattered warts about 1-1.5 × 1 μ, and non-amyloid (hyaline in Melzer's), and a low broken reticulum of broad and narrow lines most of which are in part distinctly coated with amylaceous material but on some the non-amyloid basic ornamentation visible.

Hymenium. Basidia 2-spored, 26-33 × 9-11 μ, clavate, thin-walled, hyaline in KOH; sterigmata 4-8 μ long, straight, conic, cystidia 30-37 × 4-8 μ, as crooked filaments to somewhat ventricose and with a crooked neck, hyaline, thin-walled, rarely with refractive content. Pseudoparaphyses none, basidioles abundant.

Hyphal layers. Tramal plates of loosely interwoven hyaline smooth, thin-walled non-gelatinous hyphae 5-12 μ in diam. and occasional sphaerocysts up to 20 μ present, laticiferous hyphae rare; subhymenium of *loosely interwoven much-branched* filaments 3-9 μ diam. Peridium not differentiated into layers, in young specimens about 200 μ thick and of closely interwoven, hyaline non-gelatinous hyphae 4-10 μ in diam., laticiferous hyphae interspersed and sphaerocysts rare (to apparently absent in some sections); surface with a few projecting hyphal ends but no true turf or hypodermial layer present. Clamp connections none.

Solitary on soil under duff (± 3" deep), under *Quercus garryana* north of Corvallis, Oregon. May 23, 1929. S. M. Zeller 6862.

Zeller had not identified this collection to his own satisfaction though he did place it on a sheet with other collections of *Arcangeliella rosea*.

The smaller spores, their differences in ornamentation and the amyloid reaction of the elements in both species, and the habitat difference are all significant. But the subhymenial layer shows the most basic difference. The alveolate surface of the gastrocarps is not to be regarded lightly as a character though here we are lacking information as to just what actually happens to the peridium.

46. Gymnomyces **socialis** (Hark.) Singer & Smith comb. nov.

Octaviania socialis Harkness Proc. Acad. Sci. Bot. III 1:252. 1899.

Arcangeliella socialis (Harkness) Zeller & Dodge, Ann. Mo. Bot. Gard. 22:369. 1935.

Figs. 57-59.

Fructifications depressed globose, 10-20 mm diam. or cespitose and coalescing into irregular masses 20 × 25 × 40 mm, surface smooth, cream color to pinkish, dingy ochraceous to clay color dried; sterile base distinct, stipitiform below, continued through the gleba as a slender perennrent columella of heteromerous tissue; gleba rose pink drying "pinkish buff", cavities medium sized and empty.

Spores 9-14 × 8-10(11) μ, excluding ornamentation and apiculus, globose to broadly ellipsoid, ornamented with cones 1.2-2 (2.5) μ high and 0.8-1.2 μ broad, some small particles also present, all elements of ornamentation unconnected to each other or occasionally 2-3 cones fused, strongly amyloid; sterigmal appendage present and 3-4 μ long.

Hymenium. Basidia 4-spored (rarely 2-spored), short and fat 24-28 (33) × 11-14 μ, thin-walled, readily collapsing, sterigmata curved or straight, 7-9 μ long, ± 2 μ at base; pseudoparaphyses present, ellipsoid to globose, 18-25 × 14-20 μ; cystidia rare, 26-38 × 10-14 μ fusoid-ventricose, thin-walled, smooth, content containing some refractive material.

Hyphal layers. Hyphae of tramal plates filamentous mixed with sphaerocysts (mostly sphaerocysts); subhymenium of filaments and cellular tissue interwoven into a tissue, laticiferous hyphae present; peridium with a filamentose-interwoven epicutis of hyaline hyphae, beneath this a zone of heteromerous tissue.

Hypogeous under *Eucalyptus*, *Pasania densiflora*, etc.

Material studied Parks. ♯979.

The specimen selected for study was ample, well dried, and checked in essential details with the description by Zeller & Dodge (1936, p. 623). We have not studied the co-type, so the concept established here is tentative. Harkness apparently did not describe a latex as being present and Parks, who usually indicated such a character if it were present, failed to mention its presence in his notes. Hence, we transfer the fungus to *Gymnomyces*.

47. Gymnomyces **compactus** Singer & Smith sp. nov.
Fig. 60.

Gastrocarpio 1-2 cm lato, globoso vel irregulari, albo, demum brunneomaculato; gleba alba, dein brunnea; minute loculata; sporis 10-14 × 9-12 μ, late ellipsoideis aculeolatis; aculeis amyloideis; cystidiis nullis. Specimen typicum legit prope Sandy, Oregon, 17 June 1937, S. M. Zeller *8286* (NY).

Gastrocarp 1-2 cm thick, globose to irregular, white with brownish spots, surface uneven to wrinkled; gleba white, stained brown in places, cavities small and partly empty; columella none; sterile base none.

Spores 10-14 × 9-12 μ, broadly ellipsoid; sterigmal appendage inconspicuous; ornamentation heavily amyloid, in the form of warts closely arranged in lines or fused into groups of various shapes but no long ridges or unbroken lines present, prominences about 1 μ high, very faint fine lines or streaks on spore wall also present but these scarcely visible under oil; spore wall about 0.5 μ thick and yellowish-hyaline in Melzer's; plage area not distinctive.

Hymenium. Basidia 26-33 × 9-12 μ, 4-spored; sterigmata short (-6 μ) and fine, straight; basidial wall thin and hyaline, content hyaline and protoplasmic (material preserved in liquid). Basidioles numerous. Pseudoparaphyses none. Cystidia none.

Hyphal layers. Subhymenium cellular, the cells enlarging to sphaerocysts, thin-walled, hyaline in KOH; mediostratum of interwoven hyphae with some sphaerocysts mixed in especially at junction points, filamentose hyphae with somewhat enlarged hyphal cells with thin smooth hyaline

walls. Epicutis of peridium a thin decumbent turf of dermatocystidia 18-30 × 4-7 μ, mostly narrowly fusoid to clavate (layer evident in young specimens) and with thin hyaline walls. Context (in age the entire peridium) of interwoven filamentous hyphae with subgelationous walls which are smooth and hyaline, the hyphae 4-7 μ diam. but near subhymenium scattered sphaerocysts occur. Oleiferous hyphae none. Clamp connections none.

This species was identified as *Hydnangium compactum* by Zeller.

According to Dodge & Zeller (1936) the "eo-type" of *H. compactum* Harkness has spores 5-6 μ in diameter and has a thick peridium of jellified hyphae. It probably does not belong in the Astrogastraceous Series.

48. Gymnomyces **ferruginascens** Singer & Smith sp. nov.
Fig. 61.

Gastrocarpio (7)10-50 mm lato, globoso vel ellipsoideo; peridio opaco, calcei-albo dein ferruginascente, haud viscido; gleba alba, dein pallida, brunnescente maturitate, loculata; columella stipiteque nullis, e tubereulo myceliosо nascitur; carne KOH ope ferrugineo-brunneo fit, odore debili; sporis 11-14.5 × 10-12.5 μ, hyalino-stramineis, echinatis; pseudocystidiis paucis; peridio duplici, in strato interno ex hyphis filiformibus tangentialiter dispositis constante, in strato externo ex hyphis palisadice dispositis efformato. Specimen typicum ligit prope McCall, Idaho, U.S.A. 18 Aug. 1958. Smith *60269* (MICH).

Gastrocarp (7)10-50 mm in largest diam., globose to ellipsoid or if developing among roots irregular in outline, attached at base but only by a tubercle of mycelium; peridium dry and unpolished, dull white when young, gradually becoming rusty brown especially from handling; gleba white at first, becoming pallid and by maturity "tawny" to "russet" (rusty brown), loculate, chambers empty and lined by hymenium; columella and stipe none; odor faintly disagreeable in large collections.

Spores 12-16(18) × 9-12(15) μ excluding ornamentation, ellipsoid to subglobose, ornamented with amyloid spines and warts some of which are unconnected but others fused into groups or connected by fine lines, the prominent elements 1-1.5 μ high; sterigmal appendage straight or oblique, attached centrally.

Hymenium. Basidia and basidioles forming a continuous hymenium, 35-60 × 10-14 μ, clavate, rarely ventricose in midportion, 2-, and 4-spored, very rarely 1- or 3-spored, hyaline, thin-walled, readily collapsing; sterigmata mostly slightly curved; pseudocystidia very rare, imbedded in hymenium, tibiiform, up to 7.5 μ broad.

Hyphal layers. Subhymenium strongly developed, cellular and with frequent large sphaerocysts, hyaline in well dried material or where unstained by natural color changes; mediostratum "regular" consisting of filamentose hyphae somewhat interwoven but extending in the direction of the tramal plates, not or at most only slightly gelatinized, rather loosely arranged at juncture of tramal plates and sphaerocysts evident in these areas; peridium with an epicuticular layer consisting of a palisade of versiform elements cylindric, subulate, ampullaceous, or clavate with tips varying from acute to broadly rounded, hyaline but becoming brown inside and out, with thin to thick (1.2 μ) wall, the elements of the palisade

eventually decumbent; inner peridial layer of hyaline to brownish filaments, tangential-repent, scarcely gelatinized, with thin to slightly thickened walls and narrow protoplasmic content. Hyphae all inamyloid and lacking clamp connections.

Chemical characters. $FeSO_4$ pale olivaceous on the gleba; KOH, quickly rusty brown on peridium.

Solitary to scattered under *Picea engelmanii* and *Abies lasiocarpa*.

Material studied. Idaho, Squaw Meadows, Valley County, Aug. 18, 1958, Smith-60269, type (MICH); Smith-60271, 60272, 60370, 60371, 60372, 60373 and 60598 all from the same locality.

This species is a good example to demonstrate the necessity of obtaining accurate data on fresh material to properly characterize a species of this genus. The color change is the most obvious field character, but the chemical reactions are also very important. As pointed out previously, *M. foetens* is distinguished by its odor and lack of sphaerocysts. Since the mediostratum of the tramal plates does show some sphaerocysts in the zone where branches come off, *G. ferruginascens* may be regarded as belonging in *Gymnomyces* but extremely close to *Martellia*.

49. Gymnomyces **parksii** Singer & Smith sp. nov. Figs. 62-63.

Gastroearpio 10-15 mm lato, basi stipiti formi cava praedito sed gleba columella haud perforata est, superificie alba; odore nullo; sporis 8-11 × 7-9 μ, subglobosis echinatis (echinulis 2-2.5 μ longis ad apices tantum amyloideis, reticulatione incompleta reunitis inter se). Cystidiis raris, contentu destitutis, tenui-tunicatis, subfusoideis. Specimen typicum legit prope Los Gatos, Calif. Parks *477* (*Z-27*) (NY).

Fructifications 10-15 mm broad (estimated), with a hollow stipe-like base which does not penetrate the gleba but in places the gleba is exposed in the area between the margin of the peridium and the sterile base; white, odorless.

Spores 8-11 × 7-9 μ, subglobose to broadly ellipsoid, with a prominent pointed sterigmal appendage 3-4 μ long (not included in above measurement), ornamented with prominent spines 2-2.5 μ long which are amyloid only near the apex or over upper half, and strongly amyloid lines and particles forming almost a broken reticulum at times and about 0.5 μ high.

Hymenium. Basidia 33-44 × 9-11 μ, clavate, 2- and 4-spored; sterigmata 4-6 × 2 μ, straight, conic. Cystidia rare, about 50 × 11 μ subfusoid, thin-walled, lacking any distinctive content; pseudoparaphyses none.

Hyphal layers. Mediostratum of tramal plates mostly filamentous-interwoven but sphaerocysts present as plates approach the peridium; subhymenium cellular. Peridium with an epicutis in the form of a compact (almost indistinct) trichodermium of septate hyphae 6-11 μ diam.; interior to this occurs a layer of mostly filamentose hyphae but some sphaerocysts clearly seen; laticiferous hyphae rare; clamp connections none demonstrated on the hyphae anywhere.

In heavy clay soil under oaks, Los Gatos, Calif. Parks 477 (Z-27), type (NY).

We take pleasure in dedicating this very unusual species to the collector, Mr. Harold E. Parks, who has collected so many hypogeous fungi

in California. The most interesting feature to us is that from the standpoint of gross morphology we have here a level of evolution in the Astrogastraceous Series almost exactly comparable to the *Truncocolumella* level in the *Gastroboletus* series (see Smith & Singer, 1959). *M. parksii* compares readily in this respect with *Truncocolumella citrina* var. *separans* since in both the gleba is slightly exposed around the point of attachment at maturity.

In the Zeller collections this fungus was filed under *Arcangeliella alveolata* and is now marked as packet no. 5 on that folder. It is, of course, not the same as any of the other species filed there under that name.

ELASMOMYCES Cavara

Malpighia 11:426. 1879.

This genus is characterized by the absence of both a latex and true laticiferous hyphae, by a strong differentiation of a regular filamentous mediostratum lacking distinct sphaerocysts, by the absence of clamp connections, by having amyloid spore ornamentation, and by dermatocystidia often forming a turf as an epicutis, or the epicutis in the form of a trichodermium (but not as an epithelium); a stipe-columella is present at least in a reduced state, or only a columella is present and percurrent.

Type species. *E. mattirolanus* Cavara.

As defined here species with sphaerocysts in the mediostratum of the tramal plates are excluded. From the standpoint of a level of evolution this genus is, in general, slightly more reduced in the gross morphology of the fruiting body than *Macowanites*, and extends, morphologically to a lower level, i.e., to forms which do not ever open to expose the gleba and in which the columella is at least somewhat reduced from a stipe-like structure. The degree of reduction of the columella is the main character by which the genus *Martellia* is recognized. In the latter, the columella bears no resemblance to a stipe.

KEY TO SPECIES

1. Peridium not differentiated into a cuticular layer distinct from the context and no true turf of hyphal end-cells present over the surface . . . 2
1. Cuticular layer differentiated or if not at least a distinct turf of dermatocystidia or a trichodermium present (check young specimens) . . . 5
2. Spores 15-20 × 12-15 μ, ellipsoid; odor when fresh of ethyl acetate . . . 50. *E. odoratus*
2. Spores smaller . . . 3
3. Spores 8-11 × 7-9 μ (excluding sterigmal appendage); peridium and gleba salmon-colored fresh . . . 51. *E. echinosporus*
3. Spores larger . . . 4
4. Context of peridium distinctly heteromerous . . . 52. *E. rodwayi*
4. Context of peridium with only an occasional spherical cell . . . 53. *E. mattirolanus*
5. Hymenial cystidia present . . . 6
5. Hymenial cystidia absent . . . 7
6. Spores 7-10 × 6.5-9 μ, ornamented with widely spaced bands of heavily amyloid material as well as with ridges and warts . . . 54. *E. russuloides*
6. Spores 13-16 × 12-14 μ . . . 55. *E. zellerianus*
7. Spore ornamentation in the form of a broken reticulum; odor when dried resembling that of *Lactarius camphoratus* . . . 56. *E. camphoratus*

7. Not as above 8
8. Stipe-columella present and distinct, stipe base typically pale rose color dried . . . . . 57. *E. roseipes*
8. Sterile base present; columella in the form of a percurrent structure with branches . . . . . 58. *E. pilosus*

50. Elasmomyces **odoratus** Singer & Smith sp. nov. Fig. 67.

Gastrocarpio 10-20 mm lato, concavo, impolito et albo; stipite-columella inconspicua; odor graveolens; sporis 15-20 × 12-15 μ, pallide alutaceis (in "KOH"), amyloideis; cystidiis nullis. Specimen typicum legit prope Tahoma Creek, Mt. Rainier National Park, Washington, U.S.A., 23 July 1948. A. H. Smith *29303* (MICH).

Gastrocarp 10-20 mm broad, depressed convex, whitish and unpolished; peridium not reaching the aborted stipe consistently. Stipe columella greatly reduced in proportion to size of peridium and columella not always percurrent; gleba chambered, pallid becoming pinkish cinnamon as spores mature. Odor strong of ethyl acetate.

Spores ellipsoid, 15-20 × 12-15 μ, (including ornamentation): pale cinnamon-buff in KOH, ornamentation strongly amyloid, in the form of rods or spines 1.5-2.3 μ long, thickness variable, generally amyloid over all but darker at apex or on one side as compared to the other, elements occurring in irregular ridges or lines not connected to each other except by very fine lines, isolated warts and ridges often with "tails", no true appearance of even a broken reticulum, spore wall thin and pale yellowish in Melzer's reagent where exposed; sterigmal appendage inconspicuous.

Hymenium. Basidia 1-, and 2-spored, 30-35 × 10-14 μ, clavate, readily collapsing. Basidioles numerous, with protoplasmic content. Cystidia none seen but 1-spored basidia without a spore attached resemble cystidia.

Hyphal layers. Subhymenium of vesiculose cells, 12-20 μ in diam. 1-2 cells deep. Mediostratum of filamentose-interwoven hyphae, no sphaerocysts seen. Epicutis of ochraceous hyphae 3-5 μ in diam., interwoven and appressed or at the surface with some ascending hyphal ends. Context of interwoven filaments, hyaline to yellowish, no sphaerocysts. Oleiferous hyphae none. Clamp connections none.

On humus under conifers and hardwoods, Lower Tahoma Creek, Mt. Rainier National Park, July 23, 1948. Smith 29303 type.

This species is very close to *Martellia ellipsospora* in spore characters and in its other anatomical characters but in gross morphology is quite different, being at a different level of evolution in the Astrogastraceous Series. At the present stage of our knowledge of this group it seems to us better to present the Mt. Rainier material as a new species, particularly in view of the lack of a columella in *Martellia ellipsospora*, and the fact that its gleba is not exposed, as far as we know at present.

51. Elasmomyces echinosporus (Zeller & Dodge) Zeller & Dodge, Mo. Bot. Gard. 22:370. 1935.
Macowanites echinosporus Zeller & Dodge, Ann. Mo. Bot. Gard. 6:57-58. 1919.
Fig. 65.

Gastrocarp 10 × 15 mm, even, smooth, very delicate salmon-color, becoming tawny olive in alcohol; gleba covered above, exposed below, sinuate-

about the stipe, pale salmon color like the peridium, cavities minute, irregular; stipe-columella portion not pereurrent (merely projecting up into the gleba as a conic projection.

Spores 8-11 × 7-9 μ, subglobose to broadly ellipsoid; sterigmal appendage about 2 μ long, inconspicuous, faintly amyloid over the basal portion; spore wall thickened slightly, not appreciably amyloid (hyaline in Melzer's reagent); ornamentation strongly amyloid, consisting of large to small *irregularly shaped* warts and short crooked ridges 1.2 μ to 0.25 μ high (very variable in size), many with "tails" and short side branches but *not connected to form even a partial reticulum*, often amyloid nodules arranged in crooked short chains; plage area only faintly amyloid and with only very inconspicuous ornamentation.

Hymenium continuous. Basidia clavate "2-, 4-spored, 5-8 × 11-22" Z & D. Pseudoparaphyses 23-26 × 10-13 μ, clavate, thin-walled. Cystidia "rare, clavate, apiculate, 9-10 × 20-24 μ" Z & D.

Hyphal layers. Subhymenium cellular, the cells enlarging to 10-18 μ diam. (sphaerocyst-like), thin-walled; mediostratum of interwoven filamentous tissue (as far as could be ascertained from the portion of type available). Peridium not differentiated into layers but with some hyphal ends projecting from surface as a rudimentary type of dermatocystidia, heteromerous structure more evident to the interior and interwoven connective hyphae more abundant near surface; clamp connections, none found; oleiferous hyphae rare.

Hypogeous under *Quercus agrifolia*, East Oakland, Calif. coll. N. L. Gardner (Univ. Calif. Herb. 402).

The spore ornamentation distinguishes *E. echinosporus* from *E. roseipes*. In the former, in spite of its name, the ornamentation is frequently in the form of ridges and many individual elements are branched or show distinct tails. In *E. roseipes* the elements are not as variable in height and appear as separate spines. There is also a distinct difference in habitat.

52. Elasmomyces rodwayi (Massee) Zeller, Mycologia 40:642. 1948.
Secotium rodwayi Massee, Kew Bull. Misc. Infor. 1901: 158. 1901.
Fig. 68.

Gastrocarp 20-30 mm broad, depressed globose, ochraceous-white drying dull tawny; gleba brown, firm, cavities irregular, small, exposed and depressed around the stipe; peridium continuous over the upper surface but not continuing so as to connect to the stipe hence leaving a "ring hole"; stipe (as dried) 5 mm long and 2 mm thick, hollow, lower portion furfuraceous.

Spores (7-8 μ Massee) 11-15 × 8.5-11 μ including sterigmal appendage and ornamentation; sterigmal appendage prominent, 2-3 μ long, base with a faintly amyloid jacket; ornamentation in the form of blunt cones or warts ranging in height from 1.5 μ to less than 0.5 μ, the large elements more heavily amyloid over the apex than on the sides, or some cones amyloid only at the apex, the fine amyloid particles irregularly dispersed, a few fine lines present but elements rarely connected to each other (type VI-Singer); spore wall hyaline in Melzer's reagent; plage area not different from rest of the spore surface.

Hymenium. Basidia (27)34-46 × 12-15 μ, 4-spored, clavate, becoming ventricose at or below middle when sporulating, hyaline, thin-walled. Basidioles numerous, clavate, 10-12 μ broad. Cystidia none.

Hyphal layers. Subhymenium of hyphae about the diameter of the base of the basidium, filamentose-branched but compactly interwoven, appearing cellular in sections; mediostratum of interwoven filaments 4-7 μ diam. and hyaline or nearly so in KOH, no encrusted pigment present. Epicutis of peridium poorly differentiated from context, of interwoven filamentous hyphae 3-5 μ in diam., some hyphal ends projecting at surface. Context heteromerous, sphaerocysts most abundant toward the subhymenium of the glebal cavities. Clamp connections none. Oleiferous hyphae rare.

Known only from Tasmania.

The above description is based on our study of the type, and the original description. The extent to which the stipe projects into the gleba is not too clear in the one specimen observed, but there is no evidence to indicate that it is percurrent. In this respect the species is apparently quite similar to *E. echinosporus*.

53. Elasmomyces mattirolanus Cavara, Malphigia 11:426. 1897.
Secotium mattirolanum (Cavara) Fischer in Engler & Prantl, Naturl. Pflanzenfam. 1 (Abteil. 1**: 301-2. 1900.

Gastrocarp globose-depressed or angular, 10-29 mm broad, with thin acute or rounded margin which often becomes diffracted, closed when young (according to Cavara), eventually open below or margin continuing appressed against the stipe-columella. Peridium very thin, with rudimentary cuticular layer, smooth. Context white or whitish, fragile; odor and taste not recorded.

Gleba lacunose with minute and irregular chambers, at its lower surface showing ridges radiating from the stipe-columella and sometimes covering the entire lower portion of the columella (then there is no stipe as such), and reaching the margin of the gastrocarp, apparently sometimes covered with the peridium which then connects the margin with the stipe-columella (or columella) adapting itself to the hymenophoral sublamellar ridges of the lower portion of the gleba, showing a grooved surface (false lamellae, according to Cavara, a condition we have not observed in the single type specimen at our disposal); columella constant and percurrent, adnate to the gleba, relatively short, simple, white; volva none; partial veil none seen.

Spores 10-15 × 9.5-13.5 μ, subglobose or ellipsoid and 12 × 9 μ, with central or eccentric straight or oblique sterigmal appendage; with a wall 1-1.2 μ thick, distinctly ochraceous; ornamentation of type VI (isolated spines), (0.5-) 1.5-2.5 μ high, entirely amyloid (covered with amylaceous material).

Hymenium. Basidia 30-42 × 9.5-12.5 μ, ventricose to clavate, 2- and 4-spored, with variable sterigmata but more often straight than curved and rarely very long. Sterile bodies with more or less granular incrustation, cystidioid, and varying from short and narrow to long and well differentiated (clavate, vesiculose, or cylindric) and then 22-27 × 11-12

μ, sometimes more like primordial hyphae (especially if cylindric) many transitional forms observed. Metuloids and macrocystidia none.

Hyphal layers. Subhymenium well developed and consisting of elongated as well as globose elements; lateral stratum irregular-intermixed, consisting mainly of filamentous hyphae of 2.5-4 μ diam. extending in all directions and occasional sphaerocysts (?) or merely slightly swollen hyphae (e. gr. 5.5 μ diam., shaped as shown in Cavara's original drawing) present; the mediostratum regular, consisting of similar filamentous hyphae extending more or less parallel and axial but strongly interwoven, not intermixed with sphaerocysts although occasional hyphal enlargements occur. Peridium with no distinct epicutis, the hyphae being in more parallel arrangement than those in the interior; context hyphous but with occasional vesiculose cells and air spaces, slightly gelatinized (?). Tissue of the stipe heteromerous. Laticifers none, but there are numerous oleiferous hyphae and some are broad enough to be "empty" laticifers (diameter 2.7-5.5 μ), very long, yet there is no latex, no contents or incrustation. Surface layer of stipe of suberect elongated elements. Hyphae of all tissues inamyloid, without clamp connections.

Subhypogeous under fallen needles of *Abies alba* at San Giovanni, Gualberto, Forest of Vallombroso, Toscany, Italy. F. Cavara. Autumn 1896, type (NY).

This part of the type was sent to Zeller by Cravara. The rest of the type collection is said to be in the Instituto Botanico di Napoli. Mattiroli's collection from Florence, Italy, authentic, is at the Farlow Herbarium.

Illustrations: Cavara l.c.pl. 7; Revue Mycol. 21: pl. 187, fig. 1-5; Engler & Prantl l. c. fig. 150, A-F, respectively fig. 84, A-D; Petri, Flora Ital. Cryptogama 15, fig. 6-7.

The macroscopic data were taken from the part of the type studied and supplemented by Cavara's original description. The microscopic characters were described entirely from our observations and do not coincide with Cavara's data, particularly as far as the interpretation of the hymenial elements are concerned. However, there can be no doubt but that the type collection was homogeneous and that Cavara described what he saw in his own interpretation.

54. Elasmomyces russuloides Setchell, Journ. Mycol. 13:240. 1907. Figs. 66 and 69.

Gastrocarp 10-15 mm broad, 10-12 mm high, depressed-globose to depressed convex, glabrous, white to bright red; gleba white, free from stipe, cellular within, where exposed sublamellate; stipe-columella short, fairly robust, terete, percurrent, unpolished to pruinose where surface is exposed.

Spores 7-10 × 6.5-9 μ, sterigmal appendage 1.7-2 μ long in addition; globose to subglobose; nearly hyaline in KOH and in Melzer's with a strongly amyloid ornamentation over a yellowish hyaline spore wall; ornamentation in the form of widely spaced heavily amyloid bands which sometimes cross or fuse with each other but not forming a true reticulum, or only a broken reticulum, isolated warts and short ridges also present, some faintly amyloid fine lines also present, prominences about 1 μ high, plage area with lower more fused elements of the ornamentation.

Hymenium. Basidia 2-spored, 23-28 × 9-11 μ (2-, and 4-spored, Setchell), clavate, thin-walled, hyaline in KOH; basidioles numerous. Cystidia abundant in young specimens, clavate, 40-60 × 10-12 μ, content subreticulate-refractive, hyaline in KOH, walls thin and smooth.

Hyphal layers. Subhymenium of narrow (2-3 μ) branched hyaline filaments, cell at base of basidium 4-5 μ broad, subgelatinous in KOH, (*no* sphaerocysts in subhymenium); mediostratum of tramal plates of interwoven hyaline thin-walled scarcely inflated hyphae subgelatinous in KOH, in this layer occur numerous large (5-8 μ) oleiferous hyphae which connect to the hymenial cystidia; sphaerocysts not present in this layer. Epicutis of peridium a turf (decumbent in age) of dermatopsendocystidia up to 130 μ long and 12 μ broad, clavate (much like the hymenial cystidia but often much longer). Context of intricately interwoven hyphae—mostly intertangled near the surface and there also much-branched and the hyphal cells often irregular in shape, the hyphae 2-3 μ in diam. or rarely thicker; toward the gleba the hyphae 4-5 μ in diam., the cells larger and with less branching; oleiferous hyphae numerous. Sphaerocysts none. Clamp connections none. Tissue of stipe heteromerous. Dermatopseudocystidia present on stipe surface also.

Solitary to gregarious under leaves of *Heteromeles arbutifoliae* and *Quercus agrifoliae*, Berkeley, Calif. N. L. Gardner et W. A. Setchell. (Type Setchell ♯220). Type examined.

This is a most interesting *Elasmomyces*. It is more like *Macowanites* in gross morphology but the reduction in the occurrence of sphaerocysts in the tramal plates and peridium are the anatomical characters which place it in the genus where Setchell described it. It is a curious feature that this species, which shows such a striking resemblance to a young *Russula*, also shows this striking reduction in the presence of sphaerocysts. The color of the cap varies as it does in *Russula*, buttons are white at first, become bright red as the spores mature, and in age the pigment leaches out leaving a dingy variously tinted (red to yellowish) peridium. At least this is the situation which the type collection indicates and it is certainly a common occurrence in *Russula*. Also, in the type collection, some specimens are nearly sterile. In general, however, the highly colored fruit bodies even though very young in appearance have numerous spores.

This species and *E. roscipes* are very closely related but at once distinguished by the difference in the ornamentation of the spores, and the less specialized structure of the peridium. The habitat is probably significant also.

55. Elasmomyces **zellerianus** Singer & Smith sp. nov.
Fig. 70.

Gastrocarpio 15-25 mm lato; peridio luteo-albo, impolito; gleba pallide ochracea; stipite-columella manifestis; sporis 13-16.2 × 12.6-14 μ, echinatus; aculeolis 1.5-2.5 μ longis, amyloideis; ab *E. mattirolano* praesentia dermatopseudocystidorum, superficie peridii pruinosa differt. Specimen typicum, legit prope Lake Quinault, Washington, sub coniferis, 26 Oct. 1925, coll. C. A. Brown (MICH).

Gastrocarp 15-25 mm broad, depressed-globose, with undulate margin. Peridium 0.2 mm thick, yellowish white, pruinose. Gleba with large empty

cavities and thin (0.1 mm) tramal plates, light ochraceous, drying tawny-olive to wood-brown. Stipe-columella short, thick in the stipe part, percurrent in the columella part. Context white or whitish; odor and taste not reported.

Spores 13-16.2 × 12.6-14 μ, subglobose, many yellowish, many hyaline (in KOH and ammonia), ornamentation of type VI (longspinose with isolated spines 1.5-2.5 μ, completely covered with amylaceous material; sterigmal appendage oblique as in *Russula puiggarii*.

Hymenium. Basidia 31-38 × 12-15 μ, clavate, hyaline, with two sterigmata which are almost half-sickle shaped in most basidia. Cystidia on tymenium none seen with certainty.

Hyphal layers. Subhymenium very extensive and mainly cellular, more so than in *E. mattirolanus*, consisting of a thick layer of large sphaerocysts (larger than in *Macowanites* and *Russula*), and a few elongated hyphous elements, hyaline. Mediostratum relatively narrow, slightly gelatinized, subregular in arrangement, consisting of filamentous elements or occasionally very slightly enlarged hyphal elements but sphaerocysts not seen. Peridial trama consisting of hyphae extending in all directions with some air spaces between (loosely woven), slightly gelatinous, hyaline, covered by an epicutis-like outer layer which is very thin and consists of hyphal ends which are usually periclinal in their arrangement and their terminal members are sometimes cystidioid, these dermatocystidia versiform, e. gr. cylindric-capitate, ampullaceous, etc.; dermatopseudocystidia of the macrocystidium type also differentiated in the epicutis, about 54 × 9 μ, with some loosely banded contents, long-clavate; primordial hyphae also present, granularly incrusted. Laticifers none seen. Oleiferous vessels not very prominent. Hyphae of all tissues without clamp connections and inamyloid.

Emergent under conifers, Pacific Coast States, U.S.A.

Material studied. Washington, Lake Quinault, C. A. Brown, October, 26, 1925. det. Zeller (as *E. mattirolanus*), type (MICH).

The other collection, cited by Zeller & Dodge (1936) from Waldport, Oregon, S. M. Zeller No. 7112 (NY), is probably the same as the above, but we have not studied it microscopically.

E. zellerianus is certainly closely related to *E. mattirolanus*, but nevertheless sufficiently different to be recognized. We describe it here in order to show that the type species of the genus has not as yet been found in the United States, and also in order to show that the sterile bodies in the hymenium and peridial surface are apt to come within the variability observed in *Russula* and *Macowanites*, but not *Cystangium*.

56. Elasmomyces **camphoratus** Singer & Smith sp. nov.
Fig. 64.

Gastrocarpio 6-12 mm lato, subgloboso, subfulvo, glabro, impolito; odore ei *Lactarius* camphorato simili; gleba subfulva, loculata; columella percurrente; sporis 7.5-11(12) × 6.5-8(10) μ, globosis, subreticulatis; reticulatione amyloidea. Specimen typicum, legit prope Lake Quinault, Wash. 5 Nov. 1925, C. A. Brown (MICH).

Gastrocarps 6-12 mm diam. subglobose to globose-convoluted, pale to dark tan or rusty brown, glabrous and dull, odor strong and resembling

that of *Lactarius camphoratus* (all characters from dried specimens). Peridium distinct, almost papery but not readily separating. Gleba chambered, near cinnamon-buff, the chambers empty and more or less elongated approximately vertically, possibly separating slightly from the base of the columella. Columella present, colored like the peridium, percurrent and unbranched (1 good section available).

Spores 7.5-11(12) × 6.5-8(10) μ, globose to subglobose, sterigmal appendage about 2-3 μ long, oblique, not prominent, ornamentation consisting of fine lines 0.25-0.35 μ wide, forming a broken network or system of branched and anastomosing lines with some isolated granules, major prominences rare and 0.8-1 μ high, most prominences 0.25-0.3 μ high, all elements of ornamentation strongly amyloid; the wall between the lines yellowish hyaline in Melzer's reagent.

Hymenium. Basidia 28-36 × 8-9 μ, 1-, to 4-spored, hyaline in KOH, sterigmata on 2-spored basidia often 9-12 μ long, typically straight and conic. Basidioles numerous. Cystidia 32-43 × 9-13 μ, scattered, fusoid-ventricose or broadest near the obtuse apex, thin-walled, hyaline, content homogeneous or nearly so ("empty"); one-spored basidia may be mistaken for a second type of cystidium.

Hyphal layers. Tramal plates with a mediostratum of loosely interwoven non-gelatinous hyaline hyphae, (4)8-12 μ in diam., with thin walls, lacking incrustations; subhymenium of hyphae of about the same diameter but with cross walls frequent enough to make the cells nearly isodiametric; large (9-12 μ in diam.) somewhat hyaline, refractive laticiferous hyphae also present. Sphaerocysts none seen unless some of the more enlarged subhymenial elements be so interpreted. Epicutis of the peridium a compactly arranged trichodermium of non-gelatinous hyaline to yellowish thin-walled elements of various shapes: crooked-filamentous, clavate, fusoid, or simply variously irregular (the clavate elements may proliferate to produce fusoid cells, etc.). Context of interwoven hyaline thin-walled non-gelatinous hyphae with only an occasional sphaerocyst and these not grouped into nests. Laticiferous hyphae hyaline but distinct. Clamp connections absent.

In a path in a conifer forest, Lake Quinault, Washington, Nov. 5, 1925, C. A. Brown. Identified as *Arcangeliella stephensii* by S. M. Zeller.

The epicutis is difficult to interpret unless good thin sections are obtained. There is no information to the effect that a latex was present, and since C. A. Brown studied the spores from fresh material it is to be assumed that he cut up the fresh specimens. Hence it is likely that a latex was not present, or if it was, that it was watery as in some *Lactarii* related to *Lactarius camphoratus*. We are describing the species in *Elasmomyces* because of the extreme reduction in the number of sphaerocysts present and the filamentose-interwoven mediostratum of the tramal plates coupled with the fact that there are indications that the gleba loosened slightly from the base of the columella in the one longitudinal section available for study. It is tempting, in view of the odor, to postulate a relationship to *Lactarius camphoratus*, but we prefer to postpone seriously proposing such an affinity until more data from fresh collections becomes available. A number of questions remain unanswered.

57. Elasmomyces **roseipes** Singer & Smith sp. nov.
Figs. 71-72.

Gastrocarpio 18-40 mm lato, 12-20 mm alto, margine obtuse rotundato vel acuto. Peridio tri-stratoso, externe roseo, vel roseo-vinaceo, levi, haud viscoso. Stipite a columella vix separabili, 7-14 × 3-8 mm columella inclusa, albo, ad basin vel in tota parte inferna vinaceo-roseo punctato, sicco; volva nulla. Sporis echinatis, 8.8-12 × 7.5-10 μ; pseudocystidiis paucis vel submullis; tramate hymenophorali duplici, ex parte laterali subhymenii extensi pseudoparenchymosa latissima et mediostrato angustissimo regulari consistente; peridio strato externo palisadico ex membris terminalibus hypharum vix gelatinascentium cystidiformibus gaudente; strato intermedio hyphoso ex elementis filamentosis radiatim dispositis formato; tramate ipso peridii heteromero, sphaerocystibus numerosis agglomeratis cum hyphis filamentosis; hyphis primordialibus supra stratum externum peridii repentibus, flavidis, incrustatis, angustissimis, paucis internis. Hyphis omnium typorum defibulatis. Specimen typicum, legit prope Trinidad, Calif., Chas. A. White *171* (MICH).

Gastrocarp 18-40 mm broad, 12-20 mm high, semiglobate, then convex, often somewhat irregular, but not ordinarily applanate, usually umbilicate, with acute but often (mostly) so strongly recurved peridium that the margin appears broadly rounded and often somewhat furrowed on inner side (depressed along the interlamellar spaces of the outer-lower portion of the gleba).

Peridium 1-2 mm thick, thinner towards the margin, three-layered, surface pink, salmon color or rose-vinaceous, often diffracted-scaly, especially around and on the umbilicus, often with whitish areas (faded areas ?), not glutinous, rather opaque, smooth except for marginal zone.

Gleba loculate to sublamellate, light ochraceous, forming lamella-like outer ridges which may become loose and free from the rest of the gleba but usually merely continue the more loculate internal portions, dehiscent from the columella and leaving a broad ring-hole around it, appressed to it only where the margin of the gastrocarp touches the stipe-columella, usually one side of the gastrocarp does not extend downward far enough to touch the stipe-columella and the gleba remains exposed unilaterally; gleba subfree or narrowly adnexed to the apex of the columella, 3-6 mm diam. at the thickest part.

Stipe-columella. "Stipe" not clearly distinguishable from "columella" at least when the gleba is not completely enclosed, relatively short and not (or scarcely) projecting beyond the lower level of the gastrocarp, remaining for the most part not only in the hole formed by the concave underside of the gastrocarp but above the point of real or theoretical attachment of the peridium to the "stipe" (which is at the base) hence no "true" stipe present, vinaceous pink, usually densely punctate with this color on a white background, smooth, glabrous or subglabrous, often eccentric because of the unilaterally attached peridium and then on the side that is more eccentric either attached to the gleba or gleba exposed. Both "stipe" and "columella" together about 7-15 × 3-8 mm, solid, then stuffed, equal or tapering upward. Context white, rather firm, heteromerous.

Spores 8.8-12 × 7.5-10 μ, hyaline, in oldest specimens pale yellowish, subglobose to very short ellipsoid, sterigmal appendage more frequently attached to the geometrical base of the spore rather than eccentrically, and either straight or slightly oblique, ornamentation 0.7-1 μ, projecting, of type VI, i.e., with isolated spines, entirely amyloid.

Hymenium. Basidia 35-38 × 11-14 μ, 4-spored, rarely 1-, 2-, or 3-spored, clavate, or ventricose, sterigmata either straight and conic-spinose, or slightly curved but rarely truly half-sickle-shaped. Pseudocystidia clavate to subcylindric, rare and not constantly occurring, representing the continuation of the laticiferous hyphae into the hymenium, 39-55 × 5.5-10 μ; not gloeocystidial but with loose contents which appear to be short rods, externally even or uneven, internally yellowish or hyaline, not staining blue in sulfovanillin.

Hyphal layers. Subhymenium well developed, consisting of a thin layer of some globose and some elongate very small elements, but extended into an adjacent layer (lateral trama) of larger and smaller sphaerocysts interrupted only by a small number of filamentous elements and sparing little room for the central mediostratum which is extremely narrow and consists of regularly arranged filamentous hyaline elements. Peridium consisting of three layers, (1) the outermost, which is colored with a pink dissolved pigment (in ammonia and KOH) which soon fades, and is formed by a palisade of terminal cystidioid cells; these dermatocystidia hyaline, cylindric subampullaceous, clavate or capitate, sometimes with blunt protuberances or forked, 17-31 × 3-9 μ, superimposed by scarce repent thin yellowish, strongly incrusted primordial hyphae, 2.5-8 μ diam., all these elements only very rarely with some inconspicuous yellowish granular contents; below this outermost layer which is 50-60 μ thick, follows (2) a cutis-like layer corresponding to the hypodermium of the Agaricales, consisting of subparallel to slightly interwoven repent filamentous elements slightly pinkish from dissolved pigment which soon fades, the layer about 100 μ thick; interior to it (3) the peridial context which is truly heteromerous and hyaline. Surface layer of stipe with the same structure as the surface layer of the peridium. Oleiferous hyphae present in peridium and stipe-columella. Laticiferous elements not always present but when present inconspicuous, 2.5-5 μ thick, their content similar to that of the pseudocystidia, distantly septate. Clamp connections absent. Hyphae all inamyloid, in cresyl blue some of the primordial hyphae staining deep blue. No macrocystidia of the type becoming blue in sulfovanillin present on surface of cap or stipe.

Embedded or partly erumpent in duff of spruce woods, gregarious, fruiting in July and August. California.

Material studied. California, Big Lagoon Park, Charles A. White, No. 171, type (MICH), 204 and 245, paratypes (MICH).

This species has somewhat the appearance of a *Russula* of section Rigidae (Lepidinae). The acute or obtuse margin, a very important character in *Russula* seems to have no importance here. The "veil" is perhaps not constant, and certainly not very conspicuous, but it seems to be present in some specimens connecting the upper part of the base of the stipe with the outer layer of the peridium (not seen in very young

specimens) and it may be that this indicates pseudoendocarpy, but more systematic studies on fresh or well preserved material of more different stages will be necessary to be certain.

The question of the presence or absence of laticifers vexed us for some time until we came to the conclusion that these elements are not constant in many species of the group containing *Elasmomyces* and *Arcangeliella*. There is certainly no latex in this species, and the laticifers seen by us may be merely somewhat modified oleiferous hyphae although occasionally they have quite the same appearance as they typically have in *Lactarius* or in *Arcangeliella*.

The particularly narrow mediostratum is very easy to overlook in sections where the tramal plates are not cut strictly perpendicularly. For that reason and also because of the macroscopical aspect of the fruiting bodies particularly the lamellar outer layer of the gleba in many carpophores, we have considered it practical to key out *E. roscipes* in *Macowanites* also.

58. Elasmomyces **pilosus** (Zeller & Dodge) Singer & Smith comb. nov.
Arcangeliella pilosa Ann. Mo. Bot. Gard. 22:368. 1935.
Figs. 73 and 74.

Gastrocarps 30-45 mm broad, 10-40 mm high, globose to depressed-pyriform, shrinking on drying, at first whitish, becoming reddish brown, drying citrine drab to light brownish olive or olive, unpolished to pubescent. Sterile base prominent, extended above into a branched or plate-like percurrent columella of loosely interwoven hyphae.

Spores (8)9-11.5 × 8-10 μ, globose to subglobose, ornamented, the ornamentation in the form of rods and narrow cones 1-1.5 μ high and 0.7-1 μ wide, spaced moderately far apart and unconnected with each other, readily deciduous; sterigmal appendage not conspicuous.

Hymenium. Basidia 4-spored, clavate, thin-walled; basidioles numerous; pseudoparaphyses none; cystidia abundant, aciculate, 35-50 × 7-12 μ, hyaline, thin-walled, lacking incrustations.

Hyphal layers. Subhymenium of filamentous, "glassy" hyphae in KOH; hyphae of tramal plates narrow, interwoven and gelatinous, a few oleiferous hyphae present, sphaerocysts none. Peridium 2-layered, the epicutis a palisade of dermatocystidia 30-60 × 6-9 μ, subclavate to subfusoid, with thin to slightly thickened walls (0.5 μ), not gelatinous, as dried there is much amorphous material in the layer but when individual cystidia are isolated there is no incrustation on them; inner layer thick, of gelatinous hyphae 3-8 μ in diam. and more or less interwoven; no sphaerocysts seen anywhere in the gastrocarp. Clamp connections none.

Hypogeous under oak, California, February to April.

As near as we can ascertain there was no latex reported as being present when the type collection was found and apparently Zeller and Dodge placed the collection in *Arcangeliella* on the basis of hyphae they interpreted as lactifers. The dermatocystidia do not produce a true epithelium (cellular structure). However, they are an important diagnostic character of the species, as are the hymenial cystidia which, in revived preparations, are found most abundantly in the hymenium near the perid-

ium. Since the columella is a distinct percurrent structure, we place the species in *Elasmomyces*, but closely approaching *Martellia*.

In future collections we would expect some of the gastrocarps to show the gleba separating from the columella as in the case of *Truncocolumella citrina* var. *separabilis*. In *Gymnomyces parksii* the gleba does separate slightly but in that species the columella is not percurrent. It seems to us that the situation presented here is exactly what one would expect to find in any true natural series of genera or species—a few taxa which are clean-cut intermediates between genera and which must be arbitrarily assigned to a position in the classification.

Cystangium gen. nov.

Carpophoris macroscopice eis Macowanitis simillimus sed structura sua ad Setchelliogaster accedentes. Peridii strato externo epithelio efformato; tramate hymenophorali e mediostrato regulari sed sphaerocystibus intermixto et strato laterali in subhymenium transiente, cellulari, lato; cystidiis voluminosis praesentibus vel absentia. Hyphis efibulatis; sporis subglobosis, amyloideo-echinatis, flavidis.

Species typica: *Secotium sessile* Massee & Rodway ex Rodway.

Carpophore macroscopically as in *Macowanites* but structure of the peridium remainding one of *Setchelliogaster*, the outer layer being pseudoparenchymatous; leptocystidia present or absent; mediostratum of tramal plates heteromerous; clamp connections absent; spores amyloid and ornamented as in the Russulaceae.

Macowanites, *Arcangeliella*, *Elasmomyces* and *Cystangium* form a group of genera containing species which in gross morphology are almost agaric-like and merge into those in which the gastrocarp remains closed and the stipe-columella is not developed, the sterile tissues being represented by a columella only. *Elasmomyces* and *Cystangium* are at a lower level in this scale than the other two. In fact *Cystangium* appears to be a side branch in the series because although it has basic agaric structure in the fruiting body, the type species has characters not combined in either of the agaric genera, *Russula* or *Lactarius*. It could have arisen easily from *Martellia* where the characters of the epicutis and the presence of leptocystidia occur but are not combined as they are in *C. sessile*.

KEY TO SPECIES

1. Leptocystidia rare to absent	59. *C. depauperatum*
1. Leptocystidia many and conspicuous	60. *C. sessile*

59. CYSTANGIUM **sessile** (Massee & Rodway ex Rodway) Singer & Smith comb. nov. *Secotium sessile* Massee & Rodway, Proc. R. Soc. Tasmania 1911:31. 1912.

Elasmomyces sessilis (Mass. & Rod. ex Rodway) Rodway, Proc. R. Soc. Tasmania, 1924:8. 1925.

Gastrocarp up to 20 mm broad and 10 mm high, with umbilicate apex and excavate base, depressed-globose. Peridium 0.75-2 mm thick, smooth and polished, cream colored. Gleba sublamellar to labyrinthiform with radially elongated or convolute chambers, very fragile when dried, narrowly exposed between the short stipe and the lower margin, ochraceous.

Stipe-columella percurrent and scarcely expanded at apex, free from gleba, white or concolorous with the gleba; stipe portion 3-5 × 1-2 mm, scarcely protruding from below the excavation of the lower side of the gastrocarp, smooth, equal, hollow, context fragile when dry, white; odor and taste not recorded.

Spores 9.7-15 × 9.2-13.7 μ, subglobose to very short ellipsoid, pale yellow, contents blue in cresyl blue mounts, wall 1.2 μ thick, ornamentation projecting 0.8-2.2 μ, of type VI (isolated spines), rarely spores with type IV-II, i.e., with short isolated ridges, the amylaceous matter usually but not always covering the entire spines, only in particularly long spines only the tip reacting with Melzer's reagent, sterigmal appendage rather large, usually oblique and much more often eccentric than centrally attached, no distinct amyloid smoother spot in the suprahilar region differentiated.

Hymenium. Basidia 28-31 × 12-15 μ, ventricose to clavate, (1-), 2-, 3-, (4-) spored, sterigmata 7.5-11 μ long, of various shapes and sizes (half-sickle-shaped and curved inward and upward or thin-conic-spinulose and straight although oblique). Leptocystidia conspicuous and numerous, 77-115 × 16-27 μ, ventricose-ampullaceous, hyaline, "empty" or some partially granular on the outside (but very different from primordial hyphae), most with a pale melleous resinous incrustation around the apex, with rather thin to scarcely and irregularly thickened walls (walls 0.5-1.5 μ thick, simple, hyaline), not metachromatic in cresyl blue mounts (walls lilac-violet as are those of the basidia, no colored contents), arising from a considerably lower level than the basidia, sometimes actually from the mediostratum, with rounded obtuse to more or less acute tip, strongly projecting beyond the basidia. Macrocystidia and primordial elements absent.

Hyphal layers. Subhymenium very broad and cellular, consisting mainly of sphaerocysts of variable size and often arranged in rows, continuations of the cystidial bases passing through the layer. Mediostratum relatively narrow, consisting of filamentous hyphae and some sphaerocysts over 19 μ diam., hyphae regularly arranged. Peridium consisting of a broad outer layer which is an epithelium and consists of vesiculose elements 20-45 × 17-32 μ, hyaline; inner layer heteromerous, its hyphae as in the mediostratum of the tramal plates. Laticifers none. Hyphae of all tissues inamyloid, without clamp connections.

Apparently in forested regions and subhypogeous on Mt. Wellington, Hobart, L. Rodway, No. 647, type (NY, K).

The spore size indicated by Zeller & Dodge (1936) for *Arcangeliella australiensis* (Berk. & Br.) Dodge makes it impossible to accept the contention of these authors regarding the identity of *S. sessile* with *A. australiensis*.

Some parts of the description of the microscopic characters are adapted from Cunningham (1942) who thinks that this species is a *Secotium* rather than an *Elasmomyces*. For illustrations, see Cunningham, l.c. pl. 9, fig. 3, and 34, fig. 24.

The structure of the tramal plates is more like that of *Macowanites* than *Elasmomyces*. The combination of a cellular epicutis and large

leptocystidia distinguishes the genus from *Macowanites* and the presence of sphaerocysts in the mediostratum of the tramal plates excludes it from *Elasmomyces* as we define that genus here.

We have not studied the type of *Hydnangium australiensis* and so must leave the final decision as to its relationship with *C. sessile* to later type studies, but we agree with Cunningham who insists that *Secotium sessile* is an autonomous species. Zeller in his herbarium indicated that it was identical with *Elasmomyces mattirolanus*, but as we show (see *Elasmomyces*) this disposition is unacceptable.

60. Cystangium **depauperatum** Singer & Smith sp. nov.

Gastrocarpio roseo, peridio externe maculato; columella frequenter tenui-percurrente; stipite tenui praesenti; sporis 9-13.7 × 8.2-12.5 μ, echinatis; cystidiis perpaucis, vix manifestis. Sub *Nothofagis*. Specimen typicum in Herbario Lilloano conservatum est; leg. Singer prope Penella, Chile, *M1921*.

Gastrocarp 5-20 mm high, 9-15 mm broad, either higher than broad or broader than high, ovate to irregularly vertically compressed, rarely umbilicate, underside depressed around the stipe. Peridium up to 1 mm thick, smooth, unpolished and dry, surface with pink to rose-red areas on a white background. Gleba lacunose, in places sublamellar or entirely non-lamellar, chambers small, gleba fragile, pallid to pale cream color, usually exposed on one side between the short stipe and the margin of the gastrocarp. Columella vertical or oblique, thin (0.5-1 mm in section) white, percurrent or reaching only half way where it branches and becomes indistinct from the tramal plates, not expanded if percurrent; stipe 3-6 mm long, 2-3 mm thick, present as a short ventricose basal continuation of the columella and usually eccentric in the basal cavity of the gastrocarp and often adhering to one side of it, white on the exposed area, solid. Context of peridium and stipe-columella fragile and white, unchanging on exposure, taste mild, odor none.

Spores 9-13.7 × 8.2-12.5 μ, globose to broadly ellipsoid, hyaline to pale stramineous in NH_4OH, wall at times appreciably thickened; ornamentation of isolated spines (type VI) 1-2 μ high, the amylaceous matter covering the spinules completely and the latter either straight or curved, narrowly conic to rod-shaped; sterigmal appendage typically eccentric, oblique.

Hymenium. Basidia 26-41 × 11-16.5 μ, ventricose to clavate typically 4-spored but in some gastrocarps 1- and 2- and 4-spored. Cystidia absent or some inconspicuous clavate cystidioles scattered granular content (not discoloring in sulfobenzaldehyde when lacking granular content); no conspicuous leptocystidia or macrocystidia present.

Hyphal layers. Subhymenium cellular, but consisting of small, inflated, short, somewhat irregular elements with only rarely any large sphaerocysts intermixed, at first forming a rather broad layer but in age in places rather narrow. Mediostratum regular, basically filamentous, rather narow, containing only here and there an occasional sphaerocyst. Peridium consisting of an inner tramal layer which occupies about half it's diameter and consists of mostly filamentous hyphae with few sphaerocysts intermixed, or sphaerocysts at times more or less layered; and an

outer cuticular layer distinctly epithelial in structure, consisting of vesiculose elements 20 μ or more in diameter and scattered oleiferous hyphae, the cell walls forming the outer surface of the layer giving off hyphal outgrowth about 3.5 μ thick, with or without cross walls (the entire structure reminding one of the "virescens-structure" of *Russula virescens* and allied species). All hyphae inamyloid and without clamp connections.

Chemical characters: The rose colored spots 4-4-9, later becoming 6-4-4 Maerz & Paul, become "barberry" (M. & P.) when ammonia is applied.

In the Montane (Austro-Andine) and Valdivian type forests consisting mainly of *Nothofagus*, under *N. dombeyi*, subhypogeous on soil banks at 400-800 mi. alt., in the fall. Argentina, Patagonia, Nahuel Huapi National Park, along the trail from Puerto Blest to Los Cóntros, March 14, 1959, Singer *M1806* (LIL), paratype. Chile, Llanquihué, Lago Todos los Santos, above Peulla, March 20, 1959, Singer *M1921* (LIL), type.

This species is close to *Martellia idahoensis*, but differs in having a few sphaerocysts in the mediostratum of the tramal plates, in growing under *Nothofagus* instead of spruce and fir, as well as in having a stipe-columella. *Hydnangium thaxteri* can hardly be in the same as *C. depauperatum* in view of the peridial structure as described by Zeller & Dodge, and spores which are only 7-8 μ in diameter. In placing this species in *Cystangium* we are placing greatest emphasis on the epithelial type of peridial cutis and the partly exposed gleba. The aspect of the fruit body is that of an *Elasmomyces* but sphaerocysts do occur in the mediostratum of the tramal plates.

ARCANGELIELLA Cavara

Nuov. Giorn. Bot. Ital. N. S. 7:117-128. 1900.

Spores ornamented and amyloid as in the Russulaceae of the Agaricales; cystidia in the form of pseudocystidia and macrocystidia present in the hymenium; tissue of the peridium heteromerous; epicutis of the peridium typically differentiated in some manner such as a gelatinous layer or a trichodermium; laticiferous hyphae present in the tramal plates and in the context of the peridium; stipe-columella typically present; gleba chambered and the chambers empty to partially filled with spores; gastrocarp globose to irregular with the lower margin of the peridium not always extending to the stipe thus leaving the gleba exposed around the stipe-columella at maturity; latex present.

Type species. *Arcangeliella borziana* F. Cavara.

As defined here the genus is the counterpart of *Macowanites* in gross morphology, and also anatomically with the exception that typically there are relatively few sphaerocysts in the mediostratum of the tramal plates and laticiferous hyphae are abundant. The genus, as we define it here, approaches *Lactarius* so closely that one can easily mistake its species as being aborted states of the agaric genus.

KEY TO SPECIES

1. Spore ornamentation as distinct rods and cones.
   2. Cutis of peridium of appressed gelatinous filaments 1-3.5 μ in diam. 61. *A. densa*
   2. Cutis of peridium a distinct trichodermium of pseudocystidia and gelatinized hyphal tips 62. *A. borizana*

1. Spore ornamentation more or less in the form of a reticulum.
   3. Sphaerocysts of peridial tissue with refractive somewhat thickened walls
      64. *A. crassa*
3. Sphaerocysts thin-walled 63. *A. lactarioides*

61. Archangeliella **densa** (Heim) Singer & Smith comb. nov.
3564, 1958,
Archangeliella densa Heim, Comptes rendus Ac. Sc. 246:3564. 1958.
Elasmomyces densa Heim, Rev. Mycol. Paris 24:93. 1959.

Fruit body 3-3.5 cm in widest dimension, 2.7-3 cm in narrowest dimension, 1.8-2 cm high, always ochraceous and zonate. Peridium about 1 mm thick, lubricous, viscid when wet, of filamentose septate hyphae 3-6 μ broad and lacking clamp connections; and in addition with pockets of sphaerocysts the latter measuring 30-70 μ in diam., also numerous laticiferous hyphae 5-12 μ broad, and sinuous, undulating or contorted. Cortex exuding a copious white latex very soon turning citrinous. Stipe 1-1.5 cm high, 4 mm thick, single or duplex, typically enlarged upward, solid, surface smooth, terete or creased. Columella percurrent, cylindric 5-7 mm broad. Gleba labyrinthiform, dingy flesh colored, cavities large, somewhat radiating from the columella as judged by the general orientation of the tramal plates. Flesh inodorous, after a couple of minutes the taste becoming acrid.

Basidia 35-62 × 10-12 μ, 4-, rarely 2- spored, narrowly clavate with undulating walls; sterigmata 9 × 3 μ, conic. Spores 8-9.6 × 7-8.9 μ (excl. orn.), 10-13 × 9.6-10 (with orn.), broadly ovate, scarcely asymmetric without a plage (suprahilar area ornamented much like the rest of the spore surface), ornamentation type VI (Singer system), of amyloid warts and spines isolated or with only a few fine connecting lines. Cystidia, none.

Solitary on ground in woods of *Dipterocarpus* Dai. Suteb. Cianegmoi, Thailande, alt. 100-1400, 3 et 5 XII. 1957. leg. R. Heim (Typus, M.N.H.N., Paris).

This species is a typical *Arcangeliella* and very close to the type of the genus, *A. borziana*. In *Lactarius* its closest relatives appear to be with the viscid glabrous species in which the latex changes to yellow on exposure to air. *L. delicatus* is an example. As far as Smith can tell from Heim's data and his own study of the type of *A. lactarioides*, there is no particularly close relationship to the latter, other than its general generic characters. The spore ornamentation of *A. lactarioides* is very different (a heavy amyloid reticulum), its peridium is innately fibrillose, and pseudocystidia are present in the hymenium. It is most unfortunate that Heim did not describe the detailed anatomical features of the tramal plates, or publish his Latin diagnosis with the original description in 1958.

62. Arcangeliella borziana F. Cavara, Nuov. Giorn. Bot. Ital. N.S. 7:126. 1900.
Figs. 75, 76, 77, 78, 79.

Gastrocarp 6-8 × 15-30 mm, globose to irregular or oblong, often bilobed, smooth, fairly soft but drying hard, spotted with yellow, surface

smooth and viscid, peridium not always reaching the stipe-like base (thus exposing the gleba), exuding an abundant white mild latex; gleba light rose-colored, exuding a latex; with an attenuate stipe-like base (stipe-columella not present on the fragment of the type available for microscopic study).

Spores 9-15 μ, globose to subglobose, *thin-walled* (many remain partly collapsed in Melzer's reagent), usually not showing a distinct sterigmal appendage, ornamentation in the form of strongly amylaceous rods or narrow cones 1-1.3(2) × 0.5 μ, closely spaced but unconnected, wall surface between elements of ornamentation not amyloid; spores *pale brown* in KOH.

Hymenium. Basidia 4-spored, 38-44 × 10-13 μ, clavate, hyaline, thin-walled, sterigmata 4-6 × 1.5 μ, conic, straight; pseudoparaphyses none; basidioles abundant; cystidia abundant, 40-60 × 12-18 μ, fusoid-ventricose and thin-walled, a second type also present measuring 75-125 × 10-14 μ, subfusoid to subclavate and with walls 1.2-1.7 μ thick approximately, flexuous and undulating, hyaline in KOH, content homogeneous in age, protoplasmic when young, both types relatively abundant.

Hyphal layers. Hyphae of tramal plates narrow (2-4 μ) and interwoven from branching, thickest plates are in the area near the peridium and these showing some sphaerocysts. Peridium consisting of an epicutis of a more or less distinct trichodermium of dermatopseudocystidia and gelatinized hyphal tips; the context a thick (about 200 μ) layer of narrow (1.5-3 μ) hyphae strongly gelatinized and hyaline or nearly so, laticiferous hyphae present and abundant, the content of the gelatinous hyphae of hyaline granules (in KOH) which in Melzer's reagent become dull brown as in certain species of *Hygrophorous*, the cross walls of these hyphae thickened and highly refractive in KOH; innermost layer of peridium on heteromerous tissue with hyphae having granules as described above. All hyphae inamyloid. Clamp connections absent.

In fir forests, Italy, summer.

Material studied. The fragment of the type in the Zeller Herbarium (NY).

Since this is the type species of the genus great care was observed in the study of the microscopic characters, and the microscopic data given above were all obtained from the specimen cited. The data given in the section on macroscopic characters are taken from the specimen examined and the description as translated by Zeller and Dodge (1936). These data clearly indicate that the gross morphology of the fruitification of *A. borziana* is directly comparable to that of *Macowanites*. As dried the gastrocarp is hard and black, which is to be expected because of the thick gelatinous context. The thick-walled cystidia are best observed in crushed mounts since usually only the thinner-walled apical portion projects beyond the basidia. These are not pseudocystidia since they definitely originate from the narrow hyphae of the tramal plates not from the laticiferous hyphae. A second peculiar character is the presence of pseudoamyloid granules in the hyphae.

The anatomical features as well as the gross morphology of the fruit body shows that *Arcangeliella*, as characterized by the type species, clearly belongs in the Astrogastraceous Series, and that although comparable to

Macowanites in general features, differs in possessing a latex which exudes from the fresh specimens when they are cut, just as in *Lactarius*. In other words, *Arcangeliella* is to *Lactarius* what *Macowanites* is to *Russula*, either the final stage in the evolution of the agaric genus, or the first stage of degradation of an agaric to a *Gastromycete*. Thus the Astrogastraceous Series contains two distinct lines, one connecting to *Russula* and one to *Lactarius*, but at all levels of evolution the comparable genera are extremely close to each other in all other characters.

The concept of *Arcangeliella* which we introduce here is important since it is much more restricted than that of Zeller and Dodge (1936). Particularly we exclude all species in which the presence of a latex is not indicated in the original description. Zeller and Dodge relied on the presence of laticiferous hyphae in their concept, and as we have pointed out in the detailed accounts of many of the species, these structures and the commonly occurring oleiferous hyphae in Basidiomycetes generally were confused under the one heading. It was undoubtedly this situation which led these authors to put such unrelated species as those with rusty brown spores of the *Cortinarius* and *Boletellus* types in the same genus as species with the spores of the Russulaceae. It is to Zeller's credit, however, that in his last years he realized the error but he did not live to correct it.

63. Arcangeliella lactarioides Zeller, Mycologia 39:282. 1947. Fig. 80.

Gastrocarp 25-30 mm broad, 15-20 mm high, subspherical becoming expanded, summit slightly depressed; peridium smooth, innately fibrillose, dry, pale yellowish, drying brownish, context thin especially below or at margin where it breaks away from the stipe-columella; columella percurrent, 4-6 mm broad, laticiferous hyphae present, "lactiferous" Zeller; gleba white, becoming creamy, drying brownish, exposed below, adnexed, very ventricose, cavities labyrinthiform, partly filled with spores.

Spores 8-11 × 6-7 μ, ellipsoid, rather thin-walled, ornamentation in the form of a strongly amylaceous reticulum 0.3-0.5 μ high; plage area nearly smooth, sterigmal appendage short-pointed.

Hymenium. Basidia 4-spored, 40-48 × 9-12 μ, clavate, sterigmata 3-4 × 1 μ, very short and conic; cystidia present as ends of laticiferous hyphae projecting into the hymenium (psendocystidia).

Hyphal layers. Subhymenium cellular; true laticiferous hyphae abundant in tramal plates; remainder of elements in mediostratum filamentous and interwoven and with scattered sphaerocysts through this matrix. Peridium of heteromerous tissue; the epicutis a gelatinous layer with some dermatocystidia present in it but not reviving too well at the surface. Clamp connections none.

In fir woods below timberline (elev. 7500 ft.) Diller Canyon, Mt. Shasta, Calif. (Cooke 14666, type) (NY).

Material studied. Wm. B. Cooke 14666 (type).

As Zeller stated "This species is a clear connecting link between the Gasteromycetes and *Lactarius*" (l.c., p. 283). It is even closer to *Lactarius* than is *A. borizana*, as is indicated by the reticulum of the spores.

64. Arcangeliella **crassa** Singer & Smith sp. nov.
Fig. 81.

Gastrocarpio circa 3.5 cm lato, convex-depresso, pallide alutaceo, glaber, impolito; stipite columellaque 1 cm altis, 5-8 mm crassis, pallidis; gleba sublamellata; spores 8-11 × 6.5-8 μ, reticulatis; reticulatione amyloidea; Specimen typicum, legit Cow Creek, Stanislaus National Forest, 25 Jul. 1931, Frank A. Patty (NY).

Gastrocarp (as dried) up to 3.5 cm broad, convex-depressed, pale pinkish buff (dried), glabrous but unpolished; stipe-columella 5-8 mm broad, about 1 cm high, becoming hollow in largest specimen, pallid, surface unpolished; gleba pale pinkish buff, varying lamellate to lacunose on same specimen; peridium up to 5 mm thick as dried, pale pinkish-buff within, margin remaining attached to the stipe (hence gastrocarp remaining closed, —condition shown in largest specimen) or not reaching the stipe in places thus exposing the gleba (younger specimens).

Spores ellipsoid, 8-11 × 6.5-8 μ (not including sterigmal appendage); sterigmal appendage oblique and prominent; with a nearly smooth but well marked plage with an amorphous mass of amyloid material on it; ornamentation in the form of a small-meshed reticulum or broken amyloid reticulum, prominences ± 0.25 μ high, spore wall slightly thickened and inamyloid.

Hymenium. Basidia 42-53 × 10-12 μ, pedicellate-clavate, 4-spored; sterigmata straight-conic, 4-7 μ long. Cystidia rare, pseudocystidial type, 52-65 × 7-12 μ, flexuous, often pointed at apex.

Hyphal layers. Subhymenium cellular, some cells enlarged to sphaerocyst size; hymenopodium of subparallel hyphae and 2-3 hyphae thick; yellowish in KOH; mediostratum interwoven, hyphae yellow to hyaline, enlarged cells (8-12 μ) seen in groups, but these may represent cut ends of hyphae; laticiferous hyphae abundant. Epicutis of pileus of appressed filamentose hyphae 3-6 μ broad, the outermost ochraceous in KOH but the walls smooth; context of interwoven hyaline hyphae with nests of large sphaerocysts with *refractive somewhat thickened* walls hyaline in KOH. Clamp connections none. Laticiferous hyphae very numerous.

Under duff in a coniferous forest, Stanislaus National Forest, Cow Creek, July 25, 1931. Coll. Frank A. Patty. Determined as *Arcangeliella alveolata* by Zeller & Dodge and as *Elasmomyces russuloides* by Lee Bonar.

This is a most distinctive species because of the sphaerocysts in the context having thickened somewhat refractive walls, because of the ellipsoid, reticulate spores, and because of the undifferentiated peridium—there is no layering to speak of. Although it stands out very distinct in the series as a species we have some reservations as to the proper genus in which to place it. Sections mounted in KOH give off a slightly whitish-milky dissolved substance when first mounted. This in addition to the very abundant laticiferous hyphae which resemble in content those of many species of *Lactarius* has led us to place the species in *Arcangeliella*. But there are no notes whatever with the specimen. The mediostratum of the tramal plates does not contain sphaerocysts like those found in the peridial context. Smith did note clusters of small cells which could have been the cut ends of large laticiferous hyphae. Hence, if it is ever found

that this species actually does not have a latex, it should be transferred to *Elasmomyces*.

MACOWANITES Kalchbrenner

Hedwigia 15:115. August 1876.

Macowania Kalchbrenner ex Berk. Gardner's Chronicle 5 (n.s.): 785. June 17, 1876.

Hypochanum Kalchbrenner ex Berk. Gardner's Chronicle 6 (n.s.): 140. July 29, 1876, nom. nud.

Type species. *Macowania agaricina* Kalchbr. ex Berk.

Hymenophoral trama of the fully developed carpophore consisting of a broad layer of heteromerous tissue bordered by a normally narrow or inconspicuous subhymenium, or of a narrow layer of sphaerocysts (with some connective hyphae around them) bordered by a filamentous thin hymenopodium and a subcellular subhymenium. Pseudocystidia of a type similar to the macrocystidia of the *Russulae* present in the hymenium but not necessarily blackening in sulfobenzaldehyde (bluing in sulfovanillin), these also at times present in the tramal plates as endocystidia or, more often on the surface of the peridium or stipe-columella as dermatopseudocystidia; often showing transitions to primordial hyphae, especially on the peridial surface, both pseudocystidia and primordial hyphae numerous and easily demonstrable. Oleiferous hyphae present, laticiferous vessels absent. Spores hyaline to yellow under the microscope (in water) and accumulated in the chambers of the gleba showing practically the same range of colors as in *Russula* and these shades apparently constant in each species, mostly with oblique sterigmal appendage. Sterigmata very variable in shape. Spore ornamentation amylaceous and obviously of the same origin and composition as in *Russula*, covering completely all or most of the protuberances of the spore wall, more or less echinate, warty, etc., and often showing short ridges or connecting lines. Gleba frequently with a basically lamellar or sublamellar structure but strongly anastomosing or alveolar, more rarely merely loculate and irregular, without a geotropic growth thus not allowing for free spore fall; spore deposits not obtainable. Hyphae without clamp connections, inamyloid, not gelatinized except sometimes in the outer peridial layer. Columella percurrent and continued into a free stipe without a clear separation of columella and stipe, more rarely protruding below the lower margin of the gastrocarp to produce a relatively large and conspicuous free stipe. Growing in the neighborhood of trees, particularly conifers, and at first hypogeous (between the line formed by the mineral soil and the duff), often erumpent in wet weather.

There is some difficulty as far as the generic name *Macowanites* and its nomenclatorial validity is concerned. The name originally published for the genus was *Macowania* but this is a homonym of *Macowania* Oliver in Hooker's Icon. Plant. pl. 1062, 1870 (Compositae), antedating the fungus under this name by six years and dedicated to the same South African collector, MacOwan. Kalchbrenner realized this situation very soon after the publication in Gardner's Chronicle and in a letter to Berkeley, suggested *Hypochanum* as a substitute. We doubt very much

that the substitution as published in Gardner's Chronicle one month later can be construed to be a valid *nomen novum*. It consists of one sentence: "We have received a letter from the Rev. G. Kalchbrenner in which he proposes to substitute for *Macowania* the generic name *Hypochaunum*." Since, for nomenclatorial purposes the effective author is Berkeley who did not himself substitute the generic name or even write a word of approval regarding Kalchbrenner's proposal, we believe *Hypochaunum* to be a *nomen nudum*. One may legitimately doubt that it was Kalchbrenner's intention to definitely publish this substitution in his letter; rather, he was merely making an informal suggestion to a colleague. This opinion is strengthened by the fact that roughly about the same time he wrote his own article for Hedwigia in which he proposed *Macowanites* as a new genus. On the other hand, Kalchbrenner may have been merely forgetful as is evidenced by the strange fact that six years later, 1882, he republished his *Macowanites agaricinus* as a new genus and species in Grevillea.

KEY TO SPECIES

1. Odor of garlic when fresh; known only from South Africa — 66. *M. agaricinus*
1. Odor none or various but not as above — 2
2. Gastrocarp 3-14 cm broad, viscid, tan to dark brown; odor offensive — 68. *M. magnus*
2. Not as above — 3
3. Spore ornamentation 0.8-1.3 μ or more high — 4
3. Spore ornamentation regularly lower, rarely up to 0.8 μ high — 6
4. Stipe-columella conspicuous at maturity; peridium bright yellow on the disc (if variously colored blue, purple, violet olive or yellowish see *M. americanus* also) — 69. *M. citrinus*
4. Stipe-columella reduced at maturity; peridium white to pallid at first — 5
5. Peridium lacking a differentiated epicutis (or this very reduced) — 65. *M. krjukowensis*
5. Peridial cutis complex, consisting of a basal cellular layer and above it a turf of dermatopseudocystidia — 67. *M. mollis*
6. Peridium pallid, staining clay color or tawny; taste mild — 70. *M. fulvescens*
6. Peridium often with red, pink, purple, olive or white; if white then not stained markedly as above — 7
7. Taste acrid to tardily acrid — 8
7. Taste mild and remaining so — 9
8. Macrocystidia of hymenium 40-72 × 12-19 μ; gleba white to cream color; hymenopodium poorly differentiated — 71. *M. albidigleba*
8. Macrocystidia 70-100 × 6-13 μ; gleba pale tan; hymenopodium well differentiated — 72. *M. acris*
9. Epicutis of peridium of a turf of long, sparsely branched hyphae (about 100 μ long); peridium dull fuscous-violaceus — 73. *M. fuscoviolaceus*
9. Epicutis of shorter elements and color mixed and variable in different fruits of a single collection — 10
10. Spores 9-13 × 9-12 μ — 74. *M. americanus*
10. Spores 7-10 × 6-8.5 μ — 75. *M. setchellianus*

65. Macowanites **krjukowensis** (Buchholtz) Singer & Smith comb. nov.
Secotium krjukowensis Buchholtz, Hedwigia 40:314. 1901.
Elasmomyces krjukowensis (Buch.) Sacc. & D. Sacc. Syll. Fung. 17:218. 1905.
Arcangeliella krjukowensis (Buch.) Zeller & Dodge, Ann. Mo. Bot. Gard. 22:368. 1935.
Figs. 83-85.

Gastrocarp globose or irregular, about 30 mm broad. Peridium smooth, pure white, drying warm buff to buckthorn brown (according to Zeller & Dodge), eventually somewhat furrowed at lower margin. Gleba at first either exposed or enclosed, later closed below because of the incurving margin of the gastrocarp, orange when fresh (drying clay color or tawny-olive according to Zeller & Dodge), loculate with gyrose tramal plates. Columella thin, at first percurrent, later obliterated; stipe white, short and thin, inserted in a depression on lower surface of gastrocarp and continuing the columella. Context white, with mild fungous odor.

Spores 9-11 μ in diameter, globose or subglobose, yellowish hyaline (in KOH), sterigmal appendage small and inconspicuous; ornamentation of isolated warts and rods 0.5-1.5 μ high (type VI), fairly closely spaced, amyloid (positive reaction with zinc-chloride-iodine according to Buchholtz).

Hymenium. Basidia clavate, 2-, 4-spored. Pseudoparaphyses present as clavate cells with walls about 0.5 μ thick. Cystidia aciculate, about 60-10 μ, projecting beyond the level of the basidia, contents often reticulate-amorphous, with thin walls and lacking any incrustation, aldehyde reactions unknown.

Hyphal layers. Subhymenium cellular; mediostratum of tramal plates heteromerous; oleiferous hyphae also present. Peridium with a context of heteromerous tissue, no differentiated epicutis demonstrable in sections of the type (they revived poorly, but even so some detail could be observed and we feel certain there is no epithelium, at the most a few appressed dermatocystidia). Clamp connections absent.

Hypogeous but finally erumpent, solitary or cespitose, under *Populus*, *Betula* and *Tilia*, fruiting in June. U.S.S.R. Krjukovo Station, Moscow region, F. Buchholtz, type (FH, NY).

The macroscopic data have been taken from the original accounts and the microscopical notes were by A. H. Smith and taken from a study of the type. They lack precise data on the chemical behavior of the cystidia (pseudocystidia ?) since these reactions are unreliable in material as old as this. It would be interesting to restudy material from the type locality (if it is still preserved) in order to obtain data on the type of contents seen in the cystidia and to verify the composition of the epicutis of the peridium.

Since a stipe-columella is present in at least the young stages, and since the gleba is exposed during its development at least to some extent, this species falls in the orbit of *Macowanites*, *Elasmomyces* and *Cystangium*. It cannot be identified as congeneric with *Cystangium*. In its anatomy it is similar to *Macowanites*, though it is to be admitted that in gross morphology it more closely resembles *Elasmomyces*. When we

add to this the fact that actually very little is known of the species, and we do know from Smith's observations in Idaho the gross morphology of all the secotiaceous fungi as found there varies greatly with the amount of moisture in the duff, it seems more logical at this point to place greatest emphasis on the one character which appears to be critical in separating the two genera, namely the presence or absence of sphaerocysts in the mediostratum of the tramal plates. If this character proves to be unreliable as a generic character, then it will be virtually impossible to maintain both as distinct genera. Fischer's attempt to separate *Macowanites* from *Elasmomyces* by the structure of the stipe-columella fails because heteromerous tissue is present in both.

66. Macowanites agaricinus[1] (Kalch.) Kalchbrenner, Hedwigia L5 (8): 116. 1876.

Macowania agaricina Kalchbrenner, Gardner's Chronicle 5 (n.s.): 785. 1876.

Gastrocarp 44-48 mm broad, about 30 mm high, "the size of a rather small potato," spherical-compressed (broader than high). Peridium very thin, even, smooth to somewhat rough, unpolished, dingy brown, not covering the hymenophoral structures below but projecting from the marginal zone of the peridium, (which is rounded at the edge) into the outer-lower ridges of the fertile glebal layers. Gleba sublamellar-anastomosing and cavernous in places, completely free from glebal covering below and decurrent on the stipe, open through orifices on lower side, white. Stipe cylindrical, 14-16 × 9-10 mm, smooth, solid, white; columella percurrent and somewhat ventricose, solid, white. Veil none. Context fleshy, apparently pallid-white when fresh; odor strong like that of garlic.

Spores (10.5)11.5-14(-15) × (8.5-)10.5-13 μ, short-ellipsoid to subglobose, hyaline, some with a slight citrine reflection, with an oblique sterigmal appendage symmetrically attached or much more commonly attached at an eccentric point even in young spores, ornamentation amyloaceous, consisting of a reticulum of fine lines and connecting warts, amyloaceous suprahilar spot distinct.

Hymenium continuous, consisting of fertile and sterile elements. Basidia 45-56 × 9-15 μ, ventricose to subclavate, 2- to 4-spored, rarely 1-spored; sterigmata short and half-sickle-shaped to long and straight, also long and slightly curved or short and straight, (narrowly conic), reaching 14 μ in length, most frequently curved and thicker at the base, hence agaricoid. Pseudocystidia similar in shape and origin to the macrocystidia of *Russula* (corresponding to the pseudocystidia of *Russula rosea*), content either finely granular or loosely banded (hence of the kind not expected to turn blue in sulfovanillin and not likely to be macrocystidia in the definition of that type), 50-90 × 7-10 μ, broadest in the lower half at the level of the base of the basidia, with the upper portion of the cell narrower and cylindric or gradually attenuated to a rounded, rarely subacute tip, or more or less ventricose with a frequently curved pedicel,

[1] Although it is customary to consider the gender of generic taxa feminine if they end in *ites*, we have used the masculine gender since this is the way Kalchbrenner treated it both in Hedwigia and Grevillea.

connection to oleiferous hyphae often obvious. Ends of the primordial hyphae reaching the hymenial layer and having all the characteristics of the primordial hyphae of some species of *Russula* (such as *R. murrillii*, *R. dadmunii*, and *R. punctata*), with rounded or attenuated tip, with granular incrustation, sometimes septate, about 70 × 7 μ, transitions between the two types of cystidium not infrequently observed on a single section.

Hyphal layers. Hyphae of the hymenophoral trama and the trama of the peridium of similar structure. Tramal plates with a mediostratum of heteromerous tissue, near and in the subhymenium showing a trend toward more regular arrangement with some degree of bilaterality, the sphaerocysts of the central strand surrounded by filamentous elements such as normally occur in *Russula*, oleiferous hyphae[2] and what appear to be promordial hyphae.

Tissue of the columella strictly heteromerous in structure. Outermost layers of the peridium similar to the epicutis of *Russula* spp., with a broadly gelatinized layer consisting of repent hyphae which are thin-filamentous, hyaline, smooth, and intermingled with a few elements with granular contents or granular incrustations (primordial hyphae); dermatocystidia none seen. Hyphae of all tissues inamyloid, without clamp connections.

Epigeous (at maturity) in fields among grasses at the base of old trunks of *Acacia horrida*. Somerset East, South Africa, MacOwan, February 1876, No. 1211, type (K, NY).

The fragments existing at New York are considerably better than anticipated. Some data on the fresh fungus not visible anymore in the dried specimen have been taken from the original diagnosis by Kalchbrenner since they seem to go back to MacOwan's indications.

Illustrations can be found in the first account in the Gardner's Chronicle, in Kalchbrenner's paper in Hedwigia, and in Fischer's treatment of the Gastromycetes in Engler & Prantl, second edition. Yet they are always based on the same figure.

67. Macowanites **mollis** Singer & Smith sp. nov.
Fig. 94.

Gastrocarpio 10-30 mm lato, molli albo demum subalutaceo, depresso-convexo; gleba pallide subochracea; columella percurrente; sporis 11-16 × 9-13 μ, subglobosis; cystidiis 38-56 × 5-8 μ. Specimen typicum legit D. E. Stuntz, Mt. Rainier Nat'l Park, Wash. 23 Sep 1948 (Smith—*31683*) (MICH).

Gastrocarp 10-30 mm broad, depressed globose to depressed-pileate, surface white and soft to the touch, lubricous, drying cinnamon buff to alutaceous; gleba white to buff and drying slightly paler than the peridium, moderately large, soft in consistency; stipe-columella present but

[2] These are not necessarily, or perhaps never in either Russulaceae or in the Scotiaceae, actually oil-carrying ducts since cresyl blue mounts do not show any easily demonstrable oil content in them. The term is used as an anatomical term, first introduced by Fayod, and is the only term which clearly differentiates between this kind of conducting hypha and the broader latex-conducting elements, the laticiferous vessels or laticifers, a term often misleading used for both types as found in *Russula* and *Macowanites* and also for the latex-carriers of *Lactarius*.

greatly reduced, columella part percurrent or nearly so, stipe portion 4-6 × 2-3 mm, white; peridium extending to stipe-columella or leaving a narrow to wide and irregular "ringhole" exposing the gleba.

Spores globose and 10-15 μ in diam. or 11-14(16) × 9.5-13 μ and subglobose to ellipsoid; sterigmal appendage inconspicuous; ornamentation in the form of small spines unconnected or fused in groups of 2-3, 0.6-1 μ high and ± 0.25 μ broad at base, completely covered with amylaceous material; plage area ornamented as the remainder of the surface, spore wall thin to slightly thickened.

Hymenium. Basidia 1-, and 2-spored, clavate, 24-33 × 10-13 μ, hyaline, readily collapsing. Basidioles numerous. Cystidia rare to scattered, 38-56 × 5-8 μ, filamentose-acuminate to narrowly clavate-mucronate, with a small amount of refractive content variously distributed (as seen in KOH). Pseudoparaphyses none.

Hyphal layers. Subhymenium of vesiculose elements which at maturity are 10-18 μ in diam. and form a layer 2-3 cells deep. Mediostratum of tramal plates at first (near margin of peridium) filamentose but at maturity greatly enlarged cells seen scattered through it. Cuticle complex, in the form of a modified "viresceus structure" as described by *Russula* specialists, i.e., a basal cellular layer, the cells 8-15 μ diam. over and from which there is a turf of dermatopsendocystidia mixed with branched filaments of fundamental hyphae and this layer somewhat gelatinous in KOH, the turf elements versiform—clavate, contorted, fusoid, capitate-pedicelate, etc., but generally under 30 μ long though dermatopsendocystidia may be longer. Oleiferous hyphae none. Clamp connections absent.

Collected under mixed conifers and hardwoods, Lower Tahoma Creek, Mt. Rainier National Park, Wash. Sept. 23, 1948, D. E. Stuntz collector, Sm-31683 Type.

This species is a *Macowanites* on the basis of its anatomical features but the fruiting body is that of *Elasmomyces* in that the "stipe" is greatly reduced in size and the "columella" is not always percurrent. As pointed out previously, if the two genera are distinct, the ultimate distinction must be based on the anatomical features of the mediostratum of the tramal plates of mature specimens. Thus we place Stuntz's collection in *Macowanites*.

In one fruiting body which we examined hyaline hyphae 6-8 μ in diam. were scattered through the tissues and were characterized by having clamps regularly at the cross-walls. We interpret these as the mycelium of another Basidiomycete since they were not present in all carpophores examined.

The distinctive features of this species are its soft flesh, white peridium and stipe which dry alutaceous, the very narrow elements of the spore ornamentation, and the structure of the cuticle of the peridium. No odor was noted at the time the fresh material was at hand and none is present in the dried specimens. The taste of fresh material was not recorded.

Smith—29876, collected on Lower Tahoma Creek also in Mt. Rainier National Park, by Betty and William Knowles appears to be the same

as Stuntz's collection. The data recorded from the fresh material are as follows: Gastrocarp up to 3.5 cm broad, surface glabrous, *moist*, pallid yellowish to whitish with "vinaceous buff" areas in age; columella extending to upper surface (percurrent) and flaring out there to form the thin context of the peridium; gleba whitish ("tilleul buff"). Stipe short (3-5 mm) and margin of peridium not attached to it (hence stipe and columella not "differentiated").

Spore ornamentation up to 1.25 μ long; 1-spored basidia numerous; sphaerocysts conspicuous at times in the mediostratum of the tramal plates.

All other characters check well with Stuntz's collection and since the differences are slight and quantitative only, we are referring the Knowles' collection here. The dried specimens are very similar. This species is very close to *M. krjukowensis* but differs markedly in the structure of the cuticle of the peridium and also in spore size.

68. Macowanites magnus Parks in Zeller & Dodge, Ann. Mo. Bot. Garden 22:369. 1935.

Areangeliella magna (Parks in Zeller & Dodge) Zeller, Mycologia 40:643. 1948.

Fig. 86.

Gastrocarp 30-140 mm broad, resembling a stout agaric or bolete, irregular, at first conic, then expanded and almost plane, with irregular to sinuate margins. Peridium smooth, viscid, pale tan to dark brown, drying fawn-brown to army brown or cinnamon-buff, duplex, about 250-380 μ thick. Gleba white at first, drying warm buff with vinaceous tints, spongy as in *Gautieria morchelliformis* expanded, more or less radiating from the center of the gastrocarp, free to adnexed to the stipe-columella, exposed below, cavities large, labyrinthiform. Stipe short, thick, central, 30-70 mm long, about 30 mm thick, brittle, stuffed becoming hollow, bulbous at base, abruptly attenuated below the blub, subglabrous to innately fibrillose, texture of interior homogeneous, white throughout. Context taste like a mild *Lactarius*, odor becoming pungent and offensive in age.

Spores (7.5)8.5-13.5 × 7.5-12.3 μ, globose to broadly ellipsoid, pale yellowish in dilute bases, wall 0.5 μ thick, ornamentation projecting 1-1.3 μ, in the form of a broken reticulum, the warts more or less connected by lines (type II, IIIb, or more rarely IV, IIIa).

Hymenium continuous. Basidia 35-60 × 6.5-12 μ, 4-spored or rarely 1-, 2-, 3-spored, clavate to ventricose; sterigmata either straight-conic or half-sickle-shaped as in agarics, mostly the latter. Macrocystidia (?) very scattered, narrowly clavate to fusoid, in ammonia merely granular within, 60-80 × 10-14 μ, aldehyde reactions unknown.

Hyphal layers. Subhymenium thin, intermixed but subcellular, hymenopodium strongly developed but often not clearly differentiated from either the subhymenium or the mediostratum, filamentous or with an occasional swollen element, continuous with the filamentous (connecting) hyphae of the mediostratum but the latter constantly containing some large sphaerocysts especially at the juncture of the tramal plates, i.e., with relatively more filamentous elements and relatively fewer sphaerocysts than for typical heteromerous tissue, with occasional oleiferous hyphae; laticiferous vessels none seen. Outer layer of peridium (epicutis)

entirely strongly gelatinized, very broad as revived in KOH, consisting exclusively of filamentous hyphae some of which have cystidioid end-cells which are capitate, subcapitate, ampullaceous, etc., and 3-4 μ in diam., many hyphae wavy or spiral in outline, smooth, lacking solid contents, narrow (about 1.5 μ broad); primordial hyphae, dematopseudocystidia, and ciliate dermatocystidia none. Hyphae inamyloid, without clamp connections.

Material studied. California. Santa Clara County. Parks No. 208 (part of type, courtesy of C. W. Dodge).

The description of macroscopic characters is drawn from the original description since it was found that there were misidentifications of this species in the Zeller Herbarium.

The generic position of this species puzzled us for a time. The structure of the tramal plates shows what might be regarded as a transition to *Elasmomyces*. Their appearance in good sections is often misleading since the sphaerocysts are sometimes not very numerous. To view them it helps to put moderate pressure on the cover glass to spread the sections while they are being viewed, and by this means we have been able to consistently demonstrate the sphaerocysts. The habit of the fruiting bodies must have been that of a *Russula* and not a *Lactarius* or bolete. The spore ornamentation likewise suggests a *Macowanites* rather than an *Elasmomyces*. We found only oleiferous hyphae, and consequently do not think that this species can possibly be correctly placed in *Arcangeliella*.

The collections reported from Oregon are not the same as the type. Zeller 8239 has spores with the ornamentation showing no reticulum at all, and the Agate Beach coll. (Zeller 8235) is the same as Zeller 8239, only the specimens were older and in poorer condition. It should be noted that the Zeller collections were from under *Picea* and that the type was associated with redwood. As yet we have been unable to identify the Oregon collections.

69. Macowanites **citrinus** Singer & Smith sp. nov.
Figs. 87-88.

Gastrocarpio 20-40 mm lato, albo, centro citrino vel viridulilluteo, peridio sulphati ferrici ope haud mutante, mediostrato generatim tenuiculo, hymenopodio bene evoluto, subhymenio tenui subcellulari; sporis cristulatis vel reticulatis, plerumque 9-11 × 8-10 μ, reticulatione (0.5) 1-1.3 μ alto; macrocystidiis hymenialibus nullis vel subnullis, epicuticularibus praesentibus, elementis epicutis saepe ad septa separatis liberatisque. Specimen typicum legit prope Stanley, Idaho, 19 July 1958, Smith *58942* (MICH).

Gastrocarp 20-40 mm broad, convex, usually remaining so but rarely expanding to broadly convex, leaving gleba exposed below. Peridium thin, fragile, slightly viscid, smooth, in age surface cracking into irregular plates as in *M. americanus*, exposing the thin white context or even penetrating to the gleba, white with a lemon yellow to greenish yellow disc, in age watery gray along the margin; margin incurved and in places touching the stipe-columella, acute or subacute. Gleba chambered with irregular elongate cavities, gill outlines barely visible, color cartridge

buff when freshly cut but gradually becoming pale grayish when such surfaces remain exposed. Stipe-columella 10-15 mm long, 8-11 mm thick, white and unpolished, gleba attached at the apex. Veil lacking. Context of peridium, stipe and columella white, heteromerous; odor faintly pungent, taste mild.

Spores mostly 9-11(14) × 8-10(-12) μ, stramineous in KOH, yellowish in ammonia, ellipsoid to subglobose, with oblique eccentrically attached sterigmal appendage, rarely more symmetrical, ornamentation projecting (0.5) 1-1.3 μ, typically in the form of a broken reticulum and completely covered with an amylaceous material (type II, III).

Hymenium continuous. Basidia 31-36 × 11-14 μ, 4-spored or more rarely 2-spored, sterigmata apical, half-sickle-shaped or more rarely either long-conic and straight, or irregular. Pseudocystidia rare, 48-64 × 9-11 μ, mucronate at tip in most, with oily-refractive contents (apparently not typical macrocystidia); some oleiferous hyphae may enter the lower portion of the hymenium but do not form cystidiform terminal members.

Hyphal layers. Subhymenium consisting of some elongate branched hyphae but typically of subisodiametric elements, hence cellular, thin to medium width; hymenopodium generally indistinct at maturity, when present consisting of elongated filamentous elements. Mediostratum varying, according to thickness of tramal plates, from extremely thin (so thin that it may be overlooked and the hymenopodium be taken for the filamentous mediostratum known in *Martellia* and *Elasmomyces* to very thick particularly where tramal plates connect, and in these thicker places the tissue is heteromerous in fact the sphaerocysts are abundant so that in some sections the tissue appears cellular. Epicutis of peridium well developed but scarcely differentiated into an outer and an inner layer, consisting of a turf of filaments with some oleiferous hyphae intermingled, the filaments 3-6 μ broad and many with numerous (2-4) cross walls, the cells usually irregular in shape, the filaments often breaking up at the septa and the cells becoming free; dermatopseudocystidia present, of the type known for *Russula sphagnophila*, aseptate to septate, the latter type often with homogeneous contents and thus constituting a transition to primordial hyphae, the aseptate ones rounded or narrowed to an obtuse tip, with granular or banded content which blackens in sulfobenzaldehyde, both types about 70 × 6-6.6 μ. Epicuticular elements of the center of the gastrocarp with a bright yellow pigment permeating the preparation. Context heteromerous. All hyphae inamyloid and lacking clamp connections.

Chemical reaction. $FeSO_4$ on flesh of peridium no reaction; with gleba soon grayish; with context of stipe soon gray.

Gregarious under *Pinus contorta*, Stanley Lake, Sawtooth Mts., Idaho, July 19, 1958, Smith-58942, type (MICH).

This species is amply characterized by its reaction in $FeSO_4$, spore characters and color of the peridium. Where the tramal plates are narrow (about 70 μ thick) their structure bears some resemblance to the type characteristic for *Elasmomyces* and *Martellia*, but we are not prepared to assert that this is a transitional form.

70. Macowanites **fulvescens** Singer & Smith sp. nov.
Figs. 89, 90, 92.

Gastrocarpio 20-30 mm lato, globoso; peridio albido, dein diffracto atque fulvescente, haud viscido; gleba cinnamomeoalutacea, haud libera, subtus tramate marginis peridii ubi columellam attingit, connata, e loculis a columella peridium versus radiatim dispositis consistente; columella 4 mm crassa nec in stipitem liberum continuata, non dehiscente; carne columellae albida, rupta subbrunnescente. Sporis 9.5-15.2 × 7-11.8 μ, ellipsoideis vel late ellipsoideis, ornamentatione vix prominente variabili fortiter amylacea subtiliter verrueuloso-spinulosa et interdum plus minusve reticulatim connexa obtectis. Macrocystidiis praesentibus. Subhymenio cystangii modo lato ex elementis minoribus sphaerocystibusque voluminosis efformato. Strato externo peridii trichodermio haud gelatinoso efformato, e dermatopseudocystidiis partim fulvescentibus, sulfobenzaldehydica reactione subnigrescentibus hyphisque terminalibus irregularibus interixtis efformato; fibulis nullis. Sub Piceis Abietibusque specimen typicum, legit prope McCall, Idaho, 5 Aug. 1958, Smith *5958.1* (MICH).

Gastrocarp 20-30 mm broad, globose. Peridium at first continuous and whitish, later breaking up into aerolate patches and these patches staining clay color to tawny exposing the white context beneath. Gleba about 10 mm thick at the thickest point; slightly paler than "cinnamon-buff" (buff colored), attached all along the columella down to the base where the lower edge of the peridium is intergrown with the tissue of the columella, gleba not exposed at any time (in material thus far collected), consisting of cavities more or less radiating from the columella toward the peridium but chambers irregular in shape. Columella 4 mm thick, in the type collection not continued into a stipe, percurrent. Context of peridium white, thin; of columella whitish, consistency pithy, becoming cinnamon-buff when cut; odor and taste not distinctive.

Spores 9.5-15.2 × 7-11.8 μ, pale yellow in dilute bases; broadly ellipsoid, sterigmal appendage eccentric and oblique; ornamentation projecting 0.2-0.8 μ, mostly 0.4-0.5 μ, of low almost wart-like cones which are more or less crowded into shorter or longer chains or short crests, and are usually connected by very fine amyloid lines or tail-like extensions to form a partial or broken reticulum (type VI, V, IV, IIIb, II-IV, II, VIII), plage area ornamented and often showing a diffuse amyloid spot or area.

Hymenium continuous. Basidia 35-50 × 11-16 μ, 2- and 4- spored, clavate or ventricose, sterigmata variable, straight or half-sickle-shaped. Pseudoparaphyses rather numerous, vesiculose, pseudocystidia rather numerous, content blackening in sulfobenzaldehyde, only a few practically without contents (as seen in KOH or NH_4OH), 63-110 × 13-18 μ, mostly clavate-mucronate or apex merely obtuse to subacute; leptocystidia with protoplasmic content also present, 48-64 × 18-24 μ, thin-walled, clavate-mucronate, readily collapsing (perhaps only an "empty" variant of the pseudocystidia).

Hyphal layers. Subhymenium broad, consisting of small and large sphaerocysts and a few elongated narrow elements; hymenopodium poorly developed, intermittent, filamentous; mediostratum heteromerous. Peridial trama heteromerous, epicutis consisting of a differentiated turf of dermatopseudocystidia and hyphal ends which are often irregular in out-

line or forked, not gelatinized, not originating from a hypodermial layer, tending to become fulvous, cystidioid elements with contents blackening or browning in sulfobenzaldehyde. Hyphae inamyloid, without clamp connections.

Under *Picea* and *Abies*, Brundage Mt., McCall, Idaho, August 5, 1958, Smith-59584, type (MICH).

This species is the most aberrant from the type of the genus and from the other species of *Macowanites* found in Idaho that we have encountered. It has a structure of the tramal plates which because of its extensive subhymenium, reminds one of *Cystangium* and *Elasmomyces* as well as of *Hydnangium* and *Martellia*. Although, on the other hand, there is no trace of a filamentous mediostratum. This as well as the other characters typical for *Russula* favor inserting this species in *Macowanites* unless one wishes to emphasize the absence of a free stipe to justify the erection of still another genus in this series, a solution which we wish to avoid at the present time. Depending on conditions of humidity at the time the fruit body develops, the stipe, in all these secotiaceous fungi from Idaho, including *Thaxterogaster pinque*, will vary from a more or less extended portion below the lower edge of the peridium to no extension there at all. Hence we are ready to expect that future collections will eventually show a stipe for *M. fulvescens* much like that found for *M. americanus*. The elements of the epicutis are very striking because of their ochraceous content as revived in KOH.

71. Macowanites **albidigleba** Singer & Smith sp. nov.
Figs. 91, 93.

Gastrocarpio 10-30 mm lato, convexo, haud expanso, opaco, pallido, gradatim tandem rosascente; peridio crasso, firmo, sicco; sapore miti demum tarde acri, inodoro, immutabili; gleba alba, demum pallide carneolo-alutacea, lacunosa, columellae adnata. Stipite columellaque albis. Sporis 8-11.7 × 7.5-9.7 μ, ornamentatione variabili configuratione gaudente sed constanter fere humili (0.3-0.7 μ). Macrocystidiis in epicute hymenioque praesentibus. Reactione roseola ferri sulphati in carne obvia. Sub Abietibus. Specimen typicum legit prope McCall, Idaho, 30 July 1958, Smith *59225* (MICH).

Gastrocarp 10-30 mm broad, convex, not expanding, with obtusely rounded margin, gleba exposed between margin and stipe. Peridium thick, firm, dry, moist but not viscid under moderately humid conditions, unpolished at maturity, uneven, pallid at first, slowly becoming pale dull rose-color (near "vinaceous tawny"). Gleba white until old age and then merely "pale pinkish-buff" in the interior, appearing obscurely lamellate over the exposed part, lacunose inside and with very small irregular chambers. Stipe about 10 mm long, 8-10 mm thick, white, firm, subequal, columella very broadly percurrent and gleba attached to it only near the apex. Context of peridium and stipe white, firm, taste mild at first, finally tardily acrid, odor none.

Spores 7.5-11 × 7.5-9.7 μ, pale yellowish in dilute bases, subglobose to broadly ellipsoid, sterigmal appendage oblique and eccentric, ornamentation rather variable, projecting 0.3-0.8 μ, the majority with ornamentation in the form of irregular short ridges and crests often fused or

connected by fine lines, some unconnected warts and smaller amyloid particles also present in an irregular pattern, at times almost forming a broken reticulum (type IIIb, IV, V, VI, II-IV).

Hymenium. Basidia 35-54 × 13.5-15.8 μ, 2- or 4-spored. Macrocystidia 40-72 × 12-18.5 μ, numerous, varying from fusoid to clavate and sometimes with a mucro, content banded and becoming black in sulfobenzaldehyde.

Hyphal layers. Subhymenium narrow, subcellular to cellular, with elements about as broad as the base of the basidium; hymenopodium poorly developed (1-2 hyphae broad); mediostratum heteromerous, with large and medium sized sphaerocysts abundant. Epicutis of peridium of dermatopseudocystidia having loose contents, sometimes septate, and rounded to obtuse at apex, 40-70 × 5-12 μ, contents blackening in sulfobenzaldehyde (of the type known in *Russula sphagnophila*), these located among the elements of a turf of irregular often branched hyaline hyphal ends with homogeneous content and all loosely arranged in a subgelatinous layer. Context of peridium beneath this layer similar in structure to the mediostratum of the tramal plates; all hyphae inamyloid and lacking clamp connections.

Chemical characters. $FeSO_4$ on context of peridium and stipe pinkish.

Closely gregarious under *Abies grandis*, South Fork of Lake Fork Creek, Payette National Forest, July 30, 1958, Smith-59225, type (MICH), and Sm-59722, paratype (MICH).

This species was collected along with *M. americanus* and though the cap was in perfect condition, it was not viscid. However, in KOH-preparations the turf appears gelatinous, indicating that after rains it might become viscid to the touch. It differs from *M. americanus* in the much paler gleba and tardily slightly acrid taste, paler peridium when young and poorly differentiated hymenopodium.

72. Macowanites **acris** Singer & Smith sp. nov.
Figs. 95-96.

Gastrocarpio 50 mm lato, convexo-depresso, sordide griseolo-violaceo; gleba dura, carneolo-alutacea; stipite albo, paulum ochraceo ad basin; carne alba, acri; sporis 8-11.7 × 7-9.7 μ, sat intense luteis vel flavo-ochraceis, ornamentatione variabili vel absente numquam complete reticulatis, 0.4-1 μ projiciente. Macrocystidiis hymenialibus epicuticularibus praesentibus; epicute paullum gelatinosa. Sub Picea, Idaho. Specimen typicum legit prope Stanley Idaho, 20 July 1958, Smith *58967* (MICH).

Gastrocarp 50 mm broad, convex-depressed, with decurved margin, surface dry and unpolished, variously creased. Peridium dull grayish vinaceous ("Benzo brown"). Gleba as seen from the lower side obscurely lamellate, but loculate because of the development of cross walls and veins towards the peridium, 15 mm thick in deepest part, consistency hard and firm, "pinkish-buff". Stipe 30 mm long, 20 mm at apex, bulbous and 10 mm wide at base, solid, white, unpolished, stained faintly ochraceous at base, gleba attached at apex of stipe-columella. Context of peridium and stipe and columella firm and hard, taste acrid.

Spores 8-11.7 × 7-9.7 μ, broadly ellipsoid, rather deep ochraceous in ammonia, ornamentation projecting 0.3-0.8(1) μ, mostly about 0.5-0.6 μ,

ornamentation of smaller spores (from 4-spored basidia) of cones and warts with occasional linear thin connections or tail-like extensions, or warts in series forming short chains (type VI-V-IV, VI-VIII, IV-VI-VIII); the larger spores mostly almost smooth to smooth (if smooth then amyloid, type X), with an eccentric oblique sterigmal appendage.

Hymenium continuous. Basidia 4-spored (more rarely 2-spored), hyaline revived in dilute bases, clavate, 45-66 × 11-13 μ, sterigmata curved or straight, mostly the former, 6-8 μ long. Macrocystidia 70-11 × 6-13 μ, in dilute bases often only densely granular, in sulfobenzaldehyde with blackening banded contents, fusoid, abundant, subhyaline in KOH, projecting.

Hyphal layers. Subhymenium of mostly subisodiametric small elements intermixed with some short-cylindric or irregular elements extending towards the base of the basidia, characteristically of the subcellular type. Hymenopodium consisting of filamentose hyphae extending generally in the direction of the tramal plates, somewhat interwoven, diameter of hyphae 2-3 μ. Mediostratum heteromerous, sphaerocysts predominant. Trama of peridium and stipe also heteromerous but connecting hyphae also numerous and often aggregated into small strands; outer layers of peridium well differentiated, consisting of a clearly delimited epicuticular and an inner hypodermial layer, the former of loosely arranged hyphal ends 15-40 × 2-3 μ, somewhat gelatinized and in a turflike arrangement, the elements irregular in outline or forked, interspersed with these are hypha-like dermatopsendocystidia 35-50 × 4-5 μ, their content blackening in sulfobenzaldehyde, also present are septate promordial hyphae with broadly rounded apices but without banded contents as well as other elements intermediate between primordial hyphae and dermatopseudocystidia; the hypodermial layer similar in aspect to the homologous layer in typical acrid *Russulae* (pink but bleaching quickly in ammonia and consisting of repent filamentous non-gelationous hyphae); hyphae of all parts of carpophore inamyloid and lacking clamp connections.

Chemical reactions. $FeSO_4$ with context of peridium pallid to slightly dingy.

Solitary under *Picea*, Cape Horn Summit, near Stanley, Idaho July 20, 1958, Smith-58967, type (MICH).

This species approaches *Russula* more than all the other species known since it combines a strongly acrid taste with structures in the hymenophore and peridial covering which are characteristic for typical *Russulae*. The sterigmata are those of an agaric and the spores are within the range most frequently encountered in *Russula*, rather deep yellow.

73. Macowanites **fuscoviolaceus** Singer & Smith sp. nov.
Figs. 97-98.

Gastrocarpio 30 mm lato, peridio fuscoviolaceo, marginem versus obtuse violaceo, fragili, intus albo, sapore miti; gleba labyrinthiformi vix lamellari, cavitiebus parvis angustisque, sublibera, stipite albo, ferrugineascente ad basin. Sporis 7-9.7 × 6-8.3 μ, cristatis vel reticulatis partim inter verrucas 0.3-0.7 μ altas. Macrocystidiis in hymenio epicuteque praesentibus; hymenopodio maxime e parte manifesto. Sub Abietibus. Specimen typicum legit prope McCall, Idaho, 30 July 1958 Smith *59261* (MICH).

Gastrocarp 30 mm broad, convex, obtuse, with lobed or irregular more or less obtuse margin, leaving the lower surface of the gleba almost or entirely exposed. Peridium glabrous, viscid, with uneven surface, violaceous in buttons, soon becoming fuscous-violet on disc, marginal zone dull violaceous with pallid areas. Gleba scarcely lamellate on exposed surfaces, interior labyrinthiform with small and narrow cavities, milk-white except for tawny stains around the worm holes, free from the stipe-columella. Stipe 20 mm long, 12 mm thick at apex, solid, white, stained rusty around base and worm holes. Columella percurrent. Context of peridium and stipe white, brittle in the former; taste mild.

Spores 7-9.7 × 6-8.3 μ, subglobose to very short ellipsoid, yellowish in dilute bases, ornamentation projecting 0.3-0.7 μ, rather variable, connecting lines not forming a complete network, warts often arranged in crowded rows or even fused together to form ridges (type II, IIIb, VIII, IV); sterigmal appendage oblique about 3 μ long.

Hymenium continuous. Basidia 34-51 × 11.5-15 μ, 4-spored, very rarely 2-spored, clavate; sterigmata most frequently half-sickle-shaped as in *Russula* but sometimes coarse and irregular or straight (fertile ?). Macrocystidia 40-65 × 9-16 μ, clavate, fusoid or ventricose, more rarely cylindric, obtuse to broadly rounded above, with rather loose to dense banded contents, rarely without any content, content when present turning blackish in sulfobenzaldehyde.

Hyphal layers. Subhymenium consisting of subisodiametric to short-cylindric very small hyphal cells. Hymenopodium not consistently present, filamentous, hyphae 2-3.5 μ broad, longitudinally arranged; mediostratum strongly heteromerous except in the thinner connective tramal plates where sphaerocysts are rather scattered. Trama of the peridium and stipe heteromerous, the outermost layer of the peridium about 100 μ thick, formed by a turf of long sparsely branched hyphae 2.5-4 μ thick, imbedded in a gelatinous mass (in KOH mounts), terminal cells of some filaments cystidioid, numerous dermatopseudocystidia present which stain blackish in sulfobenzaldehyde. Hypodermium absent. Hyphae inamyloid, clamp connections none seen. Surface layer of stipe with a moderate number of dermatopseudocystidia similar to those on the pileus.

Chemical reaction. $FeSO_4$ slowly pinkish-buff on the context of the peridium.

Solitary under *Abies lasiocarpa*, Payette National Forest, Idaho, July 30, 1958, coll. T. Westerdale, Sm-59261, type (MICH).

The relatively long elements of the peridial turf, the milk-white gleba and the fuscous tone in the center of the peridium are distinctive. *M. americanus* has deeper yellow gleba and spores.

74. Macowanites **americanus** Singer & Smith sp. nov. pl. 1, pl. 2, upper fig.

Species subvulgata sui loci Macowaniti fuscoviolaceo peraffinis a quo differt colore peridii magis variabili at vix centro soride fuscoviolaceo; basi stipitis ferruginascente nunquam notata; dermatopseudocystidiis in peridii stipitisque superficie reactione sulfo-aldehydica maxima e parte colorabilibus (typi macrocystidialis) pareis vel nullis; epicute peridii primum e pseudocystidiis erectis, demum e strato intermixto gelatinoso

Macowanites americanus

Upper fig. *Macowanites americanus* S. & S. × 1 Photo A.H.S.

Lower fig. *Macowanites americanus* S. & S. × 2 Photo A.H.S.

depresso cutiformi consistente; hymenopodio vix vel paulum. Specimen typicum, legit prope McCall, Idaho, 16 Jul. 1954, Smith *45032* (MICH).

Gastrocarp 10-50 mm broad, semiglobate or convex-flattened to irregular, more rarely almost applanate from the beginning, eventually often expanding to plane with a decurved margin, frequently eccentric, margin acute or sometimes (especially in specimens with strongly secotiaceous gleba) obtuse. Peridium consisting of an outer cuticle-like layer which is very thin and an interior fleshy layer which is very thin at the margin but becomes thicker as it approaches the disc (where it is 1-4 mm thick), surface glabrous, viscid at first, smooth, soon cracking into large flakes (at times so deeply as to expose the gleba), color extremely variable, pale olive yellow, pale olive, pink, lilac, lilac-purple to purplish red, sometimes unicolorous and at other times showing various mixed colors in a single group of gastrocarps, often with mixed pigments in a single peridium, whitish at times when remaining covered by the duff. Gleba basically sublamellate and attached to the apex of the stipe-columella, but very convolute and intervenose, almost alveolate in many gastrocarps and frequently some hymenophoral bands extending from the margin to the stipe-columella and decurrent there, lamellar plates radiating but not regularly so, often bent or forking at various levels and not geotropically oriented, forming some completely closed winding chambers and a majority of broad chambers open toward the lower surface, thickness of the gleba variable, very broad at the margin of the peridium, or evenly narrow to the columella, or strongly ventricose and then deeply sinuate, or on the contrary concave below and then adnate to subdecurrent, at first white, soon (in correlation with the density of the accumulated spores) more or less deeply ochraceous ("ochraceous buff"), apparently always at least partly exposed, extremely fragile.

Stipe-columella 10-30 mm long, 4-12 mm at apex, usually shorter than the width of the gastrocarp, equal or nearly so, naked, uneven, white, solid, soon becoming stuffed and finally partly hollowed, percurrent to the thickest central part of the peridium, no basal mycelial tomentum present. Veil none.

Context of peridium moderately firm at first, becoming very fragile, odor none; taste mild.

Spores 8.7-13.2 × 8.2-11.8 μ, short-ellipsoid to subglobose; the sterigmal appendage eccentrically to subcentrally attached and mostly oblique, very rarely almost straight; distinctly yellowish; ornamentation strongly amyloid, consisting of warts and short spines connected into (often straight) chains or lines by a sometimes interrupted network of fine lines and occasional short ridges (type III, II, VIII), ornamentation projecting 0.5-0.8 μ or rarely up to 1.2 μ; plage area with a dark amyloid area of amorphous material which extends to the sterigmal appendage and forms a thin short jacket around its base or up to one fourth to one third the distance toward its apex.

Hymenium continuous. Basidia 23-46 × 7-13.5 μ, mostly 23-38 × 10-13 μ, broad and relatively short, clavate, hyaline, mostly 4-spored, rarely 1-, 2-, or 3-spored; sterigmata straight to curved usually conic. Pseudoparaphyses about 22 × 18 μ, thin-walled. Pseudocystidia 40-90 × 7-11.5 μ, apparently not bluing in sulfovanillin and contents not similar to that

generally expected to turn blue in the Russulaceae, ventricose, broadest in the lower, central or upper third, or rarely ampullaceous with obtusely rounded or more rarely acute attenuated tip, originating in the lower portion of the subhymenium or the outer portion of the mediostratum. Content yellow in KOH and ammonia and visible as granular to banded loosely distributed material, numerous in young specimens but appearing more scattered in mature gastrocarps.

Hyphal layers. Subhymenium well developed, of small cellular or somewhat irregular elements, hyaline, intermixed with hyphous cystidial pedicels; hymenopodium poorly differentiated, mostly inconspicuous (sometimes absent); mediostratum varying from regular to obscurely bilateral (toward the subhymenium the elements often diverging slightly), its elements mostly very strongly inflated, or typically heteromerous. Peridial trama and that of columella and stipe typically heteromerous. Epicutis of peridium at first consisting of strongly projecting pseudocystidia arranged in a palisade, the elements gradually becoming more decumbent and tangled, subgelatinous as revived in KOH, many primordial hyphae and ordinary filamentous hyphae also present in older peridia (these often dominant); dermatopseudocystidia apparently of a non-bluing type much as the pseudocystidia of the hymenium, cylindric to clavate, 25-85 × 4-8 μ; some hyaline fusoid dermatocystidia without distinctive content or incrustation also present. Beneath the epicutis occurs a hypodermium (similar to that of *Russula*) consisting of repent filamentous hyphae but differing in containing scattered sphaerocysts. Clamp connections absent and all hyphae inamyloid.

Hypogeous to epigeous on and in deep conifer duff, often in large groups, near and under stands of *Abies*, *Picea* and *Pseudotsuga*, fruiting from July until the end of August, central Idaho, U. S. A.

Material studied: Idaho, Payette National Forest, July 16, 1954, Smith and Bigelow (Smith-45032, type MICH). Numerous additional collections from the same region made in 1954 by Bigelow, Smith and Stuntz, and again in 1958 by Smith and Westerdale. These were all accessioned under A. H. Smith's series of numbers as follows: 44032, 44033, 44980, 45032, 45034, 45035, 45051, 45052, 45053, 45055, 45116, 45118, 45119, 45120, 45121, 45123, 45124, 45126, 45175, 45177, 45616, 45617, 45618, 45619, 45621, 45749, 45821, 45822, 45823, 45824, 45825, 45826, 45827, 45828, 45829, 45831, 45833, 45834, 45835, 45836, 45839, 35840, 45842, 45843, 45844, 45845, 45846, 45847, 45848, 45852, 45862, 45863, 45868, 45870, 45871, 45878, 45894, 45915, 45949, 45975, 46028, 46071, 46072, 46074, 46095, 46097, 46117, 46426, 46481, 46674, 46762, 46778, 46911, 46912, 46986, 47150.

No. 45032 contained very young primordia as well as mature fruiting bodies. The smallest primordia were 0.8 mm and 3 mm respectively. The former did not contain any spores or recognizable hymenium and was covered by strongly elongated dermatopseudocystidia which gave it a fuzzy appearance under a lens on all surfaces including the lower surface of the gastrocarp which was not yet differentiated from the upper surface (peridium) or the surface of the ventricose stipe. The color of this primordium was pale yellow and its peridium did not yet have a gelatinous epicutis. There was a slight indication of the formation of

tramal plates indicated by the direction of the hyphal strands. In the smallest button, an intermediate stage, sporulation had just barely begun, and the gleba was already well formed and fully exposed on the underside of an almost flat pileus-like peridium. At this stage there were many pseudocystidia in the hymenium and the mediostratum was still mainly composed of filamentous hyphae which were in a more or less regularly arranged yet strongly interwoven pattern with many tramal plates close together. Among these elements there were a number of endocystidia of the pseudocystidial type and many of them were rather shortened to resemble sphaerocysts, but true sphaerocysts as seen in mature material were still exceedingly rare and scattered. Some of the filamentous elements were apparently continuations of the pseudocystidia (both hymenial and endocystidia) and the hyphous texture of the hymenophore was particularly noticeable at the forkings and anastomoses of the tramal plates which were not regularly lamellar. The hymenophoral trama, flanked by the well developed cellular layers of the subhymenium was remarkably similar to the corresponding structure of mature specimens of *Elasmomyces*.

This is the one species of the genus which has been found to such an extent that worthwhile conclusions can be drawn as to its behavior in nature. In the mountains of central Idaho it exhibits the same pattern of behavior as many of the common agarics, such as species of *Clitocybe*. Its fruiting cycle begins with occasional clusters or individuals in early to mid July and reaches a peak in August as the conifer duff dries out. After that only occasional specimens or groups of specimens are found in areas where the duff is still moist. It is not at all uncommon to find whole clusters dug out by rodents and partly eaten. In fact one day Smith found it difficult to get undamaged specimens for our records. The pattern of behavior of this species excludes any possibility that these gastrocarps are abortions of particular species of *Russula*. These observations indicate that isolated collections of the same general type of specimen are better interpreted as representing distinct species than merely aborted stages of an agaric. None of the material reported on here corresponds directly to any given species of *Russula*, but the relationship to that genus as a whole is now more obvious than ever before. Eventually, when a more complete survey of *Macowanites* has been made, it will be possible to discuss in detail its relationships with *Russula*.

75. Macowanites **setchellianus** Singer & Smith sp. nov.
Fig. 82.

Gastrocarpio 10-30 mm lato, convexo-depresso, glaber in siccato pallide fulvo; gleba palide alutacea, laemosa; columella percurrentia; sporis 7-10(11) × 6-7.5(8) μ; cystidia 42-63 × 8-12 μ. Specimen typicum, legit prope Redwood Canyon, Contra Costa County, California U.S.A. H. E. Parks, *1140* (NY).

Gastrocarp about 10-30 mm broad (estimated) broadly convex-depressed, glabrous, near pale ochraceous tawny; gleba paler than peridial surface (cinnamon-buff to pale ochraceous tawny), laemose; stipe-columella percurrent concolor with peridial surface (all data from dried specimens).

Macowanites americanus S. & S. × 1 Photo A.H.S.

Martellia idahoensis S. & S. × 1 Photo A.H.S.

Martellia monticola (Hark.) S. & S. × 1 Photo A.H.S.

Spores 7-10(11) × 6-7.5(8) μ, ellipsoid, hyaline in KOH, yellowish hyaline in Melzer's sol. except for ornamentation; ornamentation about 0.25 μ high as warts and ridges—mostly short and crooked with branches, very few fine lines, heavily amyloid; plage area not distinctive; sterigmal appendage inconspicuous.

Hymenium. Basidia 30-35 × 10-15 μ clavate, mostly 4-spored, thin-walled, hyaline in KOH, readily collapsing. Cystidia 42-63 × 8-12 μ, subcylindric to narrowly clavate, thin-walled, hyaline to yellowish in KOH, content with scattered to bunched refractive particles more or less rod-like. Basidioles numerous, broadly clavate.

Hyphal layers. Subhymenium cellular, hyaline, cell walls thin and cells 6-11 μ diam.; hymenopodium present only as 1-2 strands of narrow hyphal filaments; medio-stratum of filamentose hyphae with cells 6-9 μ broad and some sphaerocysts intermingled. Cuticle of peridium complex; basal layer cellular but cells more or less catenulate and near surface a trichodermial structure more evident, the terminal members often giving rise to versiform dermatocystidia (some of which show refractive particles and may represent dermatocystidia) of various sizes—clavate to fusoid but never as large as hymenial cystidia. Context of heteromerous hyaline tissue. Clamp connections none.

Redwood Canyon, Contra Costa County, California, H. E. Parks *1440*.

This species appears to be close to *M. fulvescens* from which it differs in narrower cylindric to narrowly clavate cystidia, smaller spores, in its association with redwood, and in the more complex structure of the cuticle of the peridium. It differs from *M. acris* in the structure of the cuticle. This species is named in honor of W. A. Setchell whose interest in these fungi materially advanced our knowledge of them.

DISCUSSION

It appears to us that *Hydnangium* as defined on the basis of the type species may be considered as the genus in which the Astrogastraceous Series originated. The possibility that the genus *Laccaria* of the Agaricales arose from the same genus seems clearly indicated from the data we have presented. The type of *Hydnangium* as recognized in this work is characterized by globose non-amyloid echinulate spores, clamp connections on the hyphae, no sphaerocysts in the peridial tissue or medio-stratum of the tramal plates, and in having a flesh-colored hymenophore. All of these are characters of *Laccaria*. *Hydnangium roseum* is so similar to the type of the genus that there may be those who dispute its position as an autonomous species. *H. soderstroemii* has a pale incarnate hymenophore, and sphaerocysts are definitely present in the peridial tissue but scattered instead of in bunches as in true heteromerous tissue. Thus this species connects the presence of sphaerocysts with the flesh-tinted gleba and the presence of clamp connections. In the fourth species, *H. nigricans*, we find the spores having a pseudoamyloid ornamentation, which intro-

duces this character to the series, but the elements are more like those found on spores of most species of *Octavianina*. Also, in this species there is apparently no incarnate tint to the gleba. Were it not for the clamp connections, this species could just as well be assigned to *Octavianina* on spore characters. Undoubtedly more species of *Hydnangium* will be discovered now that the genus can be identified readily, and it will be interesting to see how their characters fit into the pattern as established by the four we have included. At present it must be admitted that *H. soderstroemii* is the only one of the four which can legitimately be regarded as connected to the Astrogastraceous Series by a positive character. Some investigators might prefer to recognize three genera at this level, one with pseudoamyloid spores, one with sphaerocysts in the peridial tissue, and one with flesh-colored gleba but lacking sphaerocysts and having non-amyloid spore ornamentation. We believe such a division to be premature at present, and see no reason to be alarmed at the thought that two or three distinct lines of development might originate in a single genus.

At the next higher level, defined by the absence of clamp connections, we have found ten species which it appears logical to group together into a genus, *Octavianina*. Here the character of pseudoamyloid spore ornamentation is found in a number of species instead of just one, and along with it we find generally yellow to yellow-brown tints of the spore wall as viewed in KOH, and longitudinal striations on the elements of the spore ornamentation. In the genus as a whole, the elements themselves are typically coarse, sphaerocysts are more widespread in the sterile tissues, and finally, one species with a latex is known.

In *O. lutea*, *O. tuberculata*, *O. papyracea*, *O. macrospora* and *O. nigricans* sphaerocysts were not conclusively demonstrated. In all of these the spore ornamentation shows some degree of change to orange or dark red-brown in iodine (Melzer's reagent). This group clearly connects up to *Hydnangium nigricans*. In fact, because of the latter, one is inclined to question the weight given to the presence or absence of clamps in distinguishing *Octavianina* from *Hydnangium*. It is in this group that the rusty brown color of the mature gleba (as dried) is quite pronounced.

The second group in *Octavianina* consists of *O. laevis* and *O. lanigera*, two species obviously closely related to *O. lutea* and *O. tuberculata* by spore characters but further characterized by the presence of sphaerocysts in the peridial tissue. Here we have the pseudoamyloid character of the spores in combination with a truly astrogastraceous character, the presence of sphaerocysts.

The fourth group contains a single species, *O. papyracea* characterized by a latex, non-amyloid spores and no sphaerocysts. However, it remains to be seen whether some latex is not present in the *O. asterosperma* com-

plex. The color changes of the fresh peridium are such as to suggest that a hyaline latex might be present. Because there is the real possibility of a complicated situation here, we have not erected a new genus for *O. papyracea*.

It can be readily seen from the above that it is in *Octavianina* that the character patterns first appear which at the next level of complexity serve to distinguish genera. The new character which distinguishes the next level is the presence of amylaceous material over all or part of the basic spore ornamentation. At this level the presence of a latex is considered of generic importance, but the genus *Zelleromyces*, as typified by *Z. cinnabarinus* has spores with heavily amyloid ornamentation in the form of a reticulum, and sphaerocysts in the peridial tissue. Actually only one species, *Z. glabrellus* appears to entirely lack sphaerocysts, and it has the elements of the spore ornamentation about as broad as in many species of *Octavianina* only in *Z. glabrellus* the elements are so heavily amyloid as to obscure the details on their surfaces.

Among the species without a latex two groups readily stand out. Those with sphaerocysts in the mediostratum of the tramal plates and those without. The genus *Martellia* is separated from *Gymnomyces* by not having them. The number of known species at this level is over three times that at the level of *Octavianina*, and there is a tendency for greater development of the columella. In *Martellia* the degree to which the amylaceous material is present on the spore ornamentation varies greatly both as to amount and position as is shown in the spores figured. In KOH many of the spores are still rather strongly ochraceous to rusty brown, and in *M. sochneri* we find the curious combination of ochraceous tawny spores with heavily amyloid spore ornamentation. It is curious that sphaerocysts are absent in this species. In *Martellia* the differentiation of the epicutis of the peridium is rather highly developed, and curiously enough, these types are nearly all repeated at higher levels of morphological complexity, even into the Russulaceae.

Gymnomyces has fewer known species than *Martellia*, but nevertheless it appears to be in the direct line to *Russula* because of the presence of sphaerocysts in the mediostratum of the tramal plates. Also, the discrepancy in the relative number of species in each genus might well be merely a sampling artifact as far as the total world flora is concerned. There are many more species to be studied than we have included here. At all events, in *Gymnomyces* we finally have all the main characters of the genus *Russula*, with the exception of the agaric-like fruit body, combined into a gastromycetous group in which the gleba never becomes exposed. It might also be noted here that if one wished to multiply genera, *Zelleromyces* could be divided into two genera on the same character which

distinguishes *Gymnomyces* from *Martellia*. We have used the character in the latter case to try to distinguish between two genera already described, and fully recognize that genera separated by a single character, especially one of this type, are likely to be of questionable value.

At the levels considered so far the fruiting body is a tubercle either with no interior sterile tissue other than the tramal plates or this material is limited to strands or plates which may or may not extend to the peridium. The next level of evolution involves the organization of this sterile tissue into a stipe-columella. In other words, it is at this level that the gastrocarp begins to resemble an agaric fruit-body.

It is clear from our study that one can select a line of species leading to *Elasmomyces* from *Martellia*, in which line sphaerocysts are absent from the mediostratum of the tramal plates. Also, one can establish a line, in which sphaerocysts are present in the mediostratum of the tramal plates, which extends from *Gymnomyces* through *Macowanites* into *Russula*. If one were to now go back to *Octavianina*, one can there find species which could serve as the ancestral types for both these lines. It is interesting to note, here, that the line leading to *Elasmomyces* appears to end in that genus, whereas the one through *Gymnomyces* and *Macowanites* ends in *Russula*. The genus *Cystangium* may be regarded as a side branch from *Gymnomyces* which has apparently not evolved into an agaric genus. At least the correlation of cellular cuticle, large leptocystidia (in the type species) and spores of the Russulaceae is not known to us in an agaric genus or other group of Gastromycete with the possible exception of a species of *Martellia*. *Cystangium sessile* simply cannot be interpreted as a direct line in the "reduction" of any known agaric.

Macowanites easily bridges the gap between *Gymnomyces* and *Russula*. As already stated, the only character which really separates them is the presence of spore discharge in *Russula* and its absence in *Macowanites*. In the characters of the cystidia and chemical reactions of both genera we find this similarity continued. The surprising feature of the species of *Macowanites* treated here is that they do not connect up exactly with known species of *Russula*, yet in the field we are certain that the majority have been passed by as aborted *Russulae* or have actually been collected for *Russulae* and then thrown out because spore deposits could not be obtained. We have included here fewer species of *Macowanites* than we have for the *Martellia-Gymnomyces* level, but we are almost certain this is an artifact that will be cleared up by more intelligent collecting in the future. To put it another way, we believe that eventually it will be found that there are more species at the *Macowanites-Arcangeliella* level than at the *Martellia-Gymnomyces* level. In the future, in view of the information presented in this paper, it will be important to study odd collec-

tions of *Russulae*, and not simply assume because no spores are deposited that they should be discarded. If spores have been discharged, some can practically always be seen on the apex of the stipe or on the soil around the specimen.

As mentioned previously, the elements of the series are so coherent as a unit that it is difficult to imagine any one attempting to refute the idea that they form an outstanding example of a clear cut line of evolution in the Basidiomycetes. The problem of which direction evolution has progressed, however, has been the subject of debate, and a review of this problem is now in order.

First let us examine the view of Heim and Malençon, that evolution progressed from *Russula* and *Lactarius* into the Gastromycete group. If we start with the Russulaceae, as these authors did, we admit that the steps as we have shown them can be interpreted either way, in their favor or in ours. For instance, it is an easy matter to visualize the basidium losing the function of spore discharge, and hence derive *Macowanites* from *Russula*. *Gymnomyces* is then very easily derived from *Macowanites* by the loss of the stipe-columella as a structure. According to this theory, *Elasmomyces* and *Cystangium* would have to be regarded as branches off the main line in which retrogressive evolution back toward agaric types has taken place. While this is possible in theory, we regard it as unlikely because the change in the structure of the mediostratum of the tramal plates need in no way be correlated with the changes in gross morphology of the fruit body, which are admittedly under more direct pressures from environmental influences. In fact one would expect that the tramal plates would retain their basic structure since this character is not subjected to stresses of the environment.

The changes which we have shown to take place from *Gymnomyces* to *Hydnangium*, with the exception of the appearance of clamp connections, can be read either way. The presence of clamp connections in Hydnangium simply cannot be logically explained by theories of degenerative evolution. To support Heim and Malençon's point of view one would have to assert that the Astrogastraceous Series actually ends in *Octavianina* and thus avoid considering a clamped species with sphaerocysts in the peridial tissue as pertinent to the discussion. We believe this to be begging the question.

The problem of the reduction of the stipe and the eventual loss of the columella is less of a problem from the Heim-Malençon school than for those advocating the idea of progressive evolution. McKnight, in unpublished data on *Psilocybe* (Agaricales), has shown that culture conditions can cause the reduction of the stipe to an indistinct columella, and that the spores of such a gastrocarp if grown under opposite conditions will

again produce stipitate agaric fruit bodies. On the other hand, practically every known group of fungi, Ascomycetes or Basidiomycetes, in which a fruiting body is produced, has found it possible to develop a stipe, so that we are forced to the conclusion that the appearance of a stipe is one of the very common modifications of fungous fruit bodies generally and that it is doubtless a response to some very widespread stimulus. In any to the same forces that have produced it in so many other diverse types of fungous fruit-body.
event, the appearance of a stipe in this Series, we believe, can be attributed

Perhaps the greatest argument in favor of degenerative evolution is that once the basidium loses its function of spore discharge, this is not easily regained, or, to state it in another way, it is very difficult for the basidium to acquire the ability to discharge spores. A consideration of this problem is certainly in order. First, a good case can be made for the loss of this function. As the timing of all processes in the fruit body is upset by adverse environmental conditions, it is easy to visualize how the processes of the alignment of the basidia by the hymenophore can be inhibited, and how this in turn could prevent the operation of the mechanism controlling discharge. Any one with much field experience in desert or subalpine habitats knows how the fruit body can become arrested in its development by adverse changes in temperature and humidity. In time these conditions could operate to select mutations which in their pattern upset the regular process of spore discharge. Also, again, one might cite the work of McKnight who found that under varied culture conditions, a single species of agaric could be made to produce mature spores in a gastroid fruit-body in such a way as to almost insure that the spores could not be normally discharged from the basidium. Yet these same spores isolated and mated, produced mycelia which in turn produced normal agaric fruit bodies from which spores were discharged. In fact, the arguments centered around spore discharge are the strongest ones which can be advanced in favor of degenerative evolution for the members of this Series.

What can be said on the other side in relation to this character. It can be argued, for instance, that the particular *Psilocybe* in question still contains a large number of "gastromycete" genes in its make up and is actually only an agaric when grown under certain environmental conditions. It cannot be denied that there are closely related gastromycetous species, see Singer and Smith on the genus *Weraroa* (1958c). This however, again assumes that the transition to active spore discharge by the basidium is a relatively easy one to make for agarics closely related to gastromycetous forms and again points out the need for critical studies on spore discharge in such agaric forms.

Let us next consider a few field observations. Smith has encountered many species of "*Russula*" in the Western United States which when the fruit bodies were fully expanded never discharged enough spores to give a recognizable spore print though the hymenium was loaded with spores. He has also found "*Russula*" buttons buried 4-6 inches in the conifer duff and measuring 3-5 cm broad which were still almost completely enclosed, and which showed faint indications of a spore print in places where the base of the stipe-columella flared out under the gleba. These were old specimens, as judged by the condition of the context. He has also fruitings of species of *Russula* in which nearly half of the fruit bodies matured hypogeously, and deposited spores even though remaining completely buried in the duff. He has also demonstrated that species of *Macowanites* will expand like an agaric (*Russula*) if weather conditions permit, but that no spore deposits can be obtained from them. Also, we have shown that at the level where *Russula* and *Macowanites* are so easily confused, there is almost regularly a great deal of variation in the form of the sterigmata and their position on the basidium. In other words, gastroid and agaricoid types are hopelessly intermixed—possibly depending somewhat on the position of the basidium in relation to the pull of gravity.

It must be assumed, in fact it can be readily demonstrated, that in any expanded *Macowanites* gastrocarp a very large number of basidia are horizontally arranged. In view of the generally large spores of the group, it is obvious that as a basidium finally matures its spores, the weight of the latter places great strain on the wall of the sterigma at a spot near the spore, presumably the narrowest point, and that sooner or later the spore will simply break off of its own weight and fall free from the glebal tissue, and such spores could be collected as a thin spore deposit. One can thus expect to collect at least some fallen spores from a gastrocarp from which spores are not discharged in the manner of an agaric. We have evidence of this in one collection from Idaho. Also, one can reasonably expect that in the course of evolution, as such forces as that here postulated for gravity are felt, the sterigmata would become modified to more efficiently support the spore. We interpret the curved conic sterigmata as such a modification.

The important point as we see it, is that at least for the Russulaceae, a sudden mutation to functional spore discharge need not be assumed. It seems to us more logical to believe that spore discharge as found in the Russulaceae has arisen by a series of minor mutational steps, first by the spore breaking free of the basidium at the weakest point on the sterigma, then possibly being helped a little at the critical moment by a slight amount of pressure from the protoplasm. Further local changes in the

strength of the wall in the sterigma, which may be associated with greater thickening of the spore wall in the part referred to as the sterigmal appendage, may have taken place, and that this all finally led up to a regularly functioning mechanism of discharge which as a set of genetic characters was stable. If there is any survival value to be attributed to more effective means of spore dispersal, the spores which broke off and were carried away would be more effective than those remaining in the gleba. Hence any genetic tendency as a result of minor local mutations in the fungus fruit body which aided in this process by causing a weak spot in the sterigmal wall, or caused protoplasmic pressure to vary slightly at a late stage in the age of the basidium, would have a tendency to be preserved by the survival value accruing to the process in its entirety.

Although we have limited our discussion here to the Astrogastraceous Series, it can at once be recognized that if this pattern holds for this group, it could equally well apply to the other series on which we have already published. It is the case of a general response to one type or kind of stimulus at a comparable level in all secotiaceous fungi so far discussed. The principles and forces are the same throughout. At this point it seems to us that the critical need now as we have already stated, is for a painstaking and critical study of spore discharge on species where the secotiaceous genera "meet" the agaric genera. In the meantime we are not inclined to admit that the mere fact of spore discharge is a major consideration either way as far as the direction of evolution in the Astrogastraceae is concerned. We consider it highly probable that in this group we have admirable material in which to study this phenomenon in detail at a less specialized level than in such groups as *Coprinus* and other highly specialized Hymenomycetes.

If progressive evolution from gastroid to agaricoid types is assumed, how does the data fit the theory? First, if we start from *Hydnangium* we have a group of Hymenogastrales which has typically colored, ornamented spores and clamp connections on the hyphae. These characters connect *Hydnangium* to a known group of other Hymenogastraceous fungi, namely *Hymenogaster*, on the one hand, and at the same time on the other hand show diverging tendencies toward a group of Agaricales not included in the Astrogastraceae, the genus *Laccaria*, as well as one species showing the character of sphaerocysts in the peridial tissue, a positive astrogastraceous character. Here we are not lacking for possible sources of origin for the line in question, and we have one species which could well be regarded the type from which the Astrogastraceae originated. From here on the pattern of discontinuities which lead toward the Russulaceae is typical of what one finds in a truly natural line of organisms, and can be read "upward" with less difficulty than "downward". For instance,

Elasmomyces and *Cystangium*, from this point of view are simply side branches from the main line leading to *Russula*, and retrogressive evolution need not be assumed. From the progressive point of view, it is easy to see how the diagnostic characters of the Russulaceae developed. Those who argue degenerative evolution for the series simply avoid this important question or try to derive the Russulaceae from the Hygrophoraceae through the tenuous connection of *Bertrandia* and *Bertrandiella*. Actually Heim (1959) has recently emphasized this idea further in his description of *Bertrandiella*. However, after studying the data he has presented we are forced to admit that we cannot agree that there is a reasonable connection here. There are three outstanding characters of the Russulaceae: The heteromerous pileus trama, the amyloid spore ornamentation and the lack of clamp connections. As can be seen *Bertrandiella*, has none of these characters. Heim illustrates clamp connections at the base of the basidium, describes the spores as having pseudoamyloid granules beneath the endospore, and describes the context of the pileus as filamentose. The characters which our colleague emphasises in pointing out the supposed relationship to the Russulaceae are the presence of a latex, a character not essential to a definition of the Russulaceae and one found in numerous unrelated Basidiomycetes such as *Mycena*, one undescribed species of *Crepidotus* (known to Smith), and apparently *Lentodium squamosum* in addition to *Lactarius* and *Bertrandia*. Thus this character could at best serve Heim's purpose only in a supporting role assuming other basic characters were present to make the relationship more likely. As for the pseudoamyloid particles in the spores, these apparently resemble pseudoamyloid particles found in the hyphae of certain species of *Hygrophorus* as pointed out by Smith and Hesler in their studies of this genus. It is almost a rule that when laticiferous hyphae are well developed they project into the hymenium as pseudocystidia. This is evident in *Mycena* and *Lentinellus*. Hence the presence of these structures, unsupported by the presence of the truly definitive characters of the Russulaceae, cannot be used as an argument in favor of a relationship in that direction. The russuloid aspect of the fruiting body can likewise be dismissed as merely a superficial resemblance. In short, we are forced to conclude that there are no basic similarities between the Russulaceae and the Hygrophoraceae (including Bertrandiella), and our statement still stands that there is no plausible phylogenetic connection between the Russulaceae and any other family of the Agaricales.

The evolutionary steps as we have presented them appear remarkably similar to those one usually finds in large groups of species, i.e., various combinations of characters—some building up to new characters, such as the heteromerous type of peridial tissue, and others disappearing

from the line, as for instance the pseudoamyloid reaction of the spore ornamentation. To our way of thinking it is very important to show how the characters of the Russulaceae could have evolved, and the interpretation of this series from the standpoint of progressive evolution is the only one which meets this criterion. It is also the only explanation which accounts for the isolated position of the Russulaceae among the gill fungi.

Since the hypothesis of progressive evolution from an Hymenogastraceous ancestor meets the most important considerations squarely and reasonably, it is the one to which we subscribe. We believe that this interpretation is strengthened by the evidence that *Laccaria*, a genus of the Tricholomataceae with spores remarkably similar to those of some Russulaceae but with entirely in-amyloid ornamentation, had its origin in the same primitive genus as the Russulaceae. It should be noted also that all these considerations are based on *Gastromycetes* in which the gastrocarp itself has not become modified for spore dispersal.

SPECIES EXCLUDED FROM THE ASTROGASTRACEOUS SERIES

1. *Arcangeliella africana* (Lloyd) Zeller & Dodge, Ann. Mo. Bot. Gard. 22:365. 1935. This species has been transferred to *Neoscecotium*, see Singer & Smith (1960).

2. *Arcangeliella ambigua* Zeller & Dodge, Ann. Mo. Bot. Gard. 22:365. 1935. This species has been transferred to *Chamonixia* see Smith & Singer (1959).

3. *Arcangeliella behrii* (Harkness) Zeller & Dodge, Ann. Mo. Bot. Gard. 22:366. 1935. A Harkness collection from Sausilito, California has been studied, and the following data recorded: Spores 11-16(18) × 9-14(16) μ, ellipsoid to truncate-elliptic, verrucose, *pale dingy straw color* in KOH, *dark red-brown* in Melzer's reagent, with a thick outer layer which is areolate-craeked in its outer part, with a thin darker brown inner layer. Basidia 2-, and 3-spored, 30-35 × 9-11 μ, elavate or slightly ventricose in mid-portion when sporulating, thin-walled and readily collapsing; basidioles numerous, no pseudoparaphyses present; cystidia rare, about 47 × 13 μ, fusoid-ventricose, thin-walled and readily collapsing, content homogeneous; hyphae of the tramal plates 3-6 μ in diameter, subparallel; thin-walled, yellow-hyaline in KOH; peridium (none was present on material available for study); clamp connections absent.

Conclusions. This is a most peculiar species by virtue of its spore characters but certainly not belonging in the Astrogastraceous Series. It may belong in the Gastroboletus Series near *Chamonixia*.

4. *Arcangeliella becari* (Petri) Zeller & Dodge, Ann. Mo. Bot. Gard. 22:366. 1935. We cannot make a positive statement in regard to this species at the present time, but place it here because of the "yellow" spores and "amber brown" gleba, characters which indicate that the species may belong to some other series.

5. *Arcangeliella caudata* Zeller & Dodge, Ann. Mo. Bot. Gard. 6:49-52. 1919. Smith & Singer (1959) have transferred this to *Chamonixia*.

6. *Arcangeliella camphellae* Berk. & Br. in Zeller & Dodge, Ann. Mo. Bot. Gard. 22:366. 1935. The type and one specimen studied (J. B. Cleland, 13). The following data were taken from the type. Spores 7-9 × 4-4.5 μ, oval in face view, varying to subelliptic, *some* in profile view obscurely inequilateral, pale rusty brown in KOH and minutely verrucose to subreticulate (very inconspicuously so under oil), wall about 0.5 μ thick, no differentiation in wall at apex.

Details of the hymenium not evident from revived material; hyphae of tramal plates of gelatinous interwoven hyaline narrow (3-4 μ) hyphae; peridium of interwoven, thin-walled, filamentous hyphae 2-6 μ in diameter and not gelatinous, no incrusting pigment present and no differentiation into layers evident; clamp connections apparently absent (but condition of the material was such as to leave some doubts as to whether they might be present but rare).

Conclusion. The data obtained from the above collections check well with the description, hence the question of different species concepts is not involved here. The spores exclude the species from the Astrogastraceous Series and point to *Hymenogaster*.

7. *Arcangeliella ellipsoidea* Zeller & Dodge, Ann. Mo. Bot. Gard. 22: 367. 1935. A portion of the type has been studied and the following data obtained. Spores 10-12.5 × 6-7.5 μ, subelliptic to obscurely inequilateral in profile view, ovate to elliptic in face view, rich tawny in Melzer's reagent, rusty brown in KOH from a thickened colored endosporium, episporium hyaline to yellowish and perforated with tawny plugs of material (episporium a pale colored layer), apex with a broad thin callus or apex almost truncate (at times with a hyaline apical blister). Basidia 20-24 × 6-7 μ, 2-, and 4-spored, hyaline, mostly collapsed; pseudoparaphyses present, inflated, 12-18 μ in diameter; cystidia, some seen and these resembling collapsed mucronate "chrysocystidia" but without a refractive content; hyphae of tramal plates interwoven, hyaline, thin-walled and loosely interwoven (revived in KOH); peridium a thick (about 180 μ) layer of interwoven filaments 3-8 μ in diameter, much-branched, hyaline in KOH, thin-walled and smooth, some oliferous hyphae seen, surface region possibly a rudimentary trichodermium of branched hyphae (not well-revived); no sphaerocysts present; clamp connections none.

Conclusions. This species is not a member of the Astrogastraceae We believe it to be an *Hymenogaster*, which is where it was originally placed by Rodway. Its proper position awaits a monograph of that genus.

8. *Arcangeliella violacea* (Massee & Rodway) Zeller & Dodge, Ann. Mo. Bot. Gard. 22:369. 1935. The specimen from the Massee collection in the Zeller material is the one reported on here. Spores 7-9.5 × 5.5-6.5 μ, ellipsoid, rusty brown in KOH and in Melzer's reagent, walls thickened somewhat, surface roughened in the manner of a *Cortinarius*—minutely warty-rugulose, no pore or plage at the apex.

Basidia 4-spored, 24-32 × 7-9 μ, hyaline, thin-walled, readily collapsing; basidioles numerous but no pseudoparaphyses seen; cystidia none; hyphae of tramal plates poorly revived but apparently subparallel; peridium lacking a gelatinous surface layer (epicutis), (but this may have been torn off when specimens were sliced for drying), a hypodermium-

like layer was all that was left and consisted of brown-walled elongated but inflated cells 12-15 μ broad; clamp connections present.

Conclusion. This is a species of *Hymenogaster*, in which genus it was originally described.

9. *Arcangeliella vulvaria* (Petri) Zeller & Dodge, Ann. Mo. Bot. Gard. 22:369. 1935. No material studied. We exclude this species tentatively on the basis of the ochraceous tawny gleba and yellow spores, and by the apparent lack of sphaerocysts in the peridium and tramal plates. We interpret the statement in Zeller & Dodge (p. 629, 1936) "gelified with abundant large lactiferous ducts" as having a coma after gelified.

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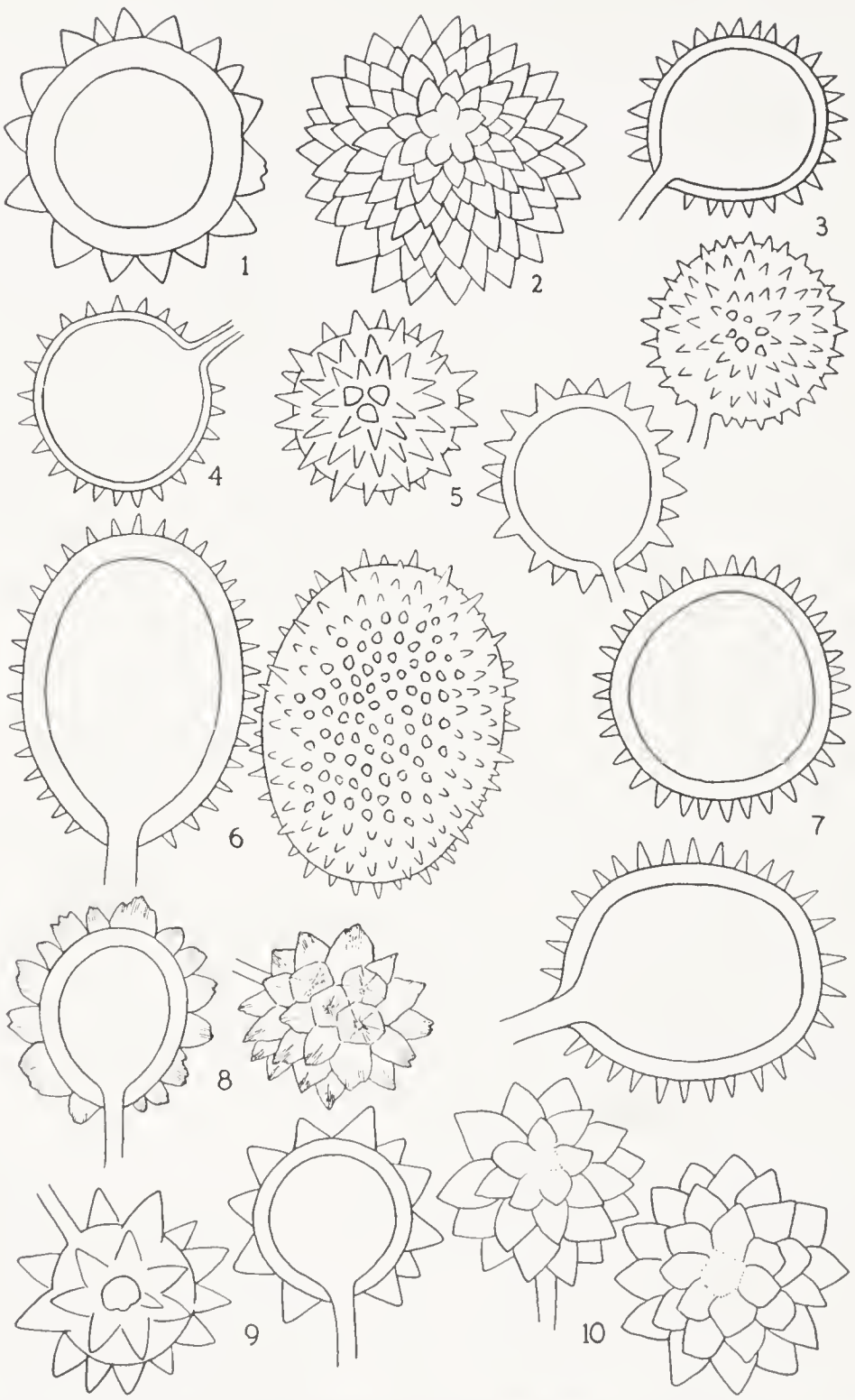

Figs. 1-10. Spores of *Hydnangium* and *Octavianina*, x 1200.

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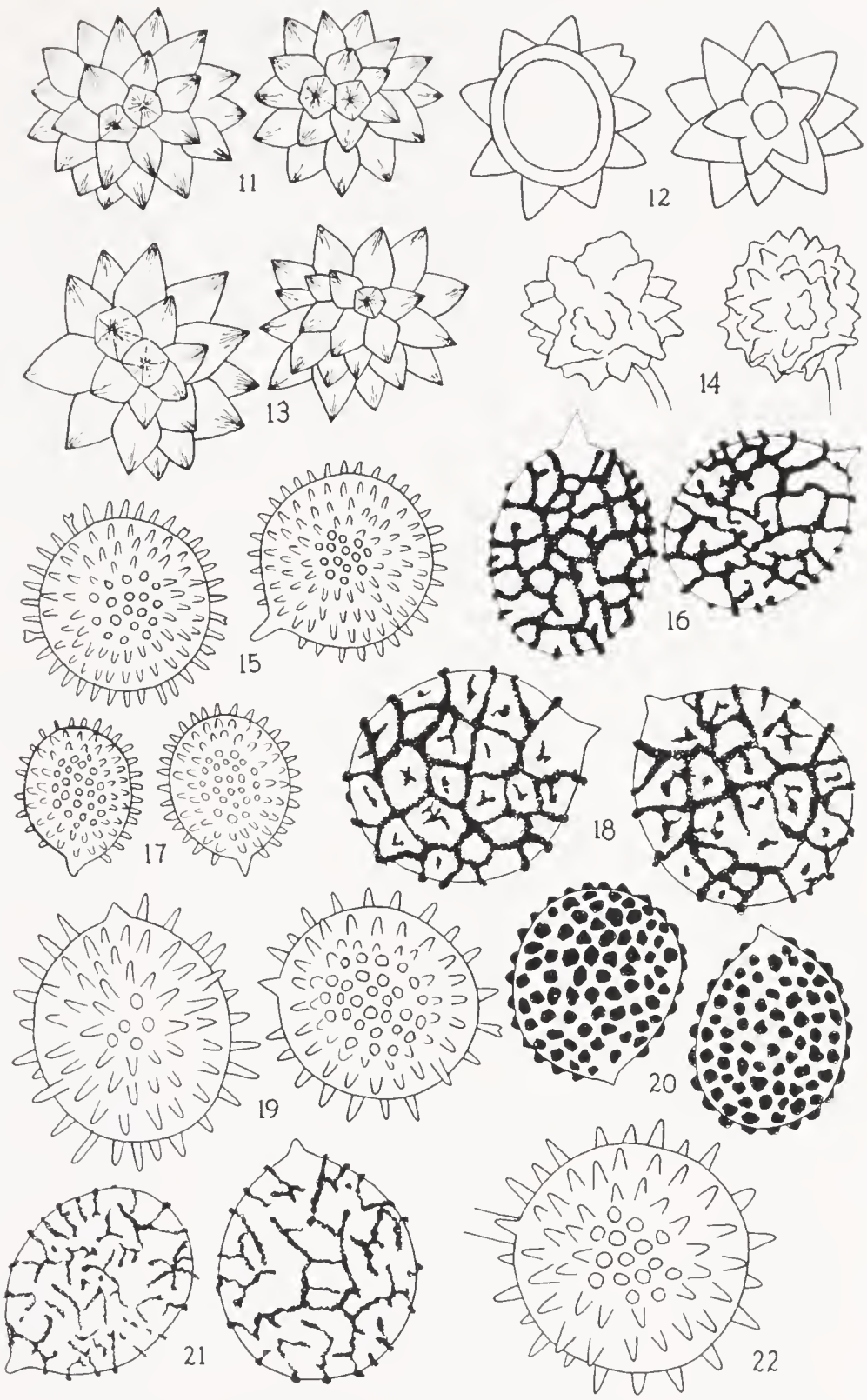
The details of the spore ornamentation are semi-schematic, especially for the smaller spores with complicated ornamentation. Hence the descriptions are to be considered more accurate as regards fine detail. A. H. Smith.



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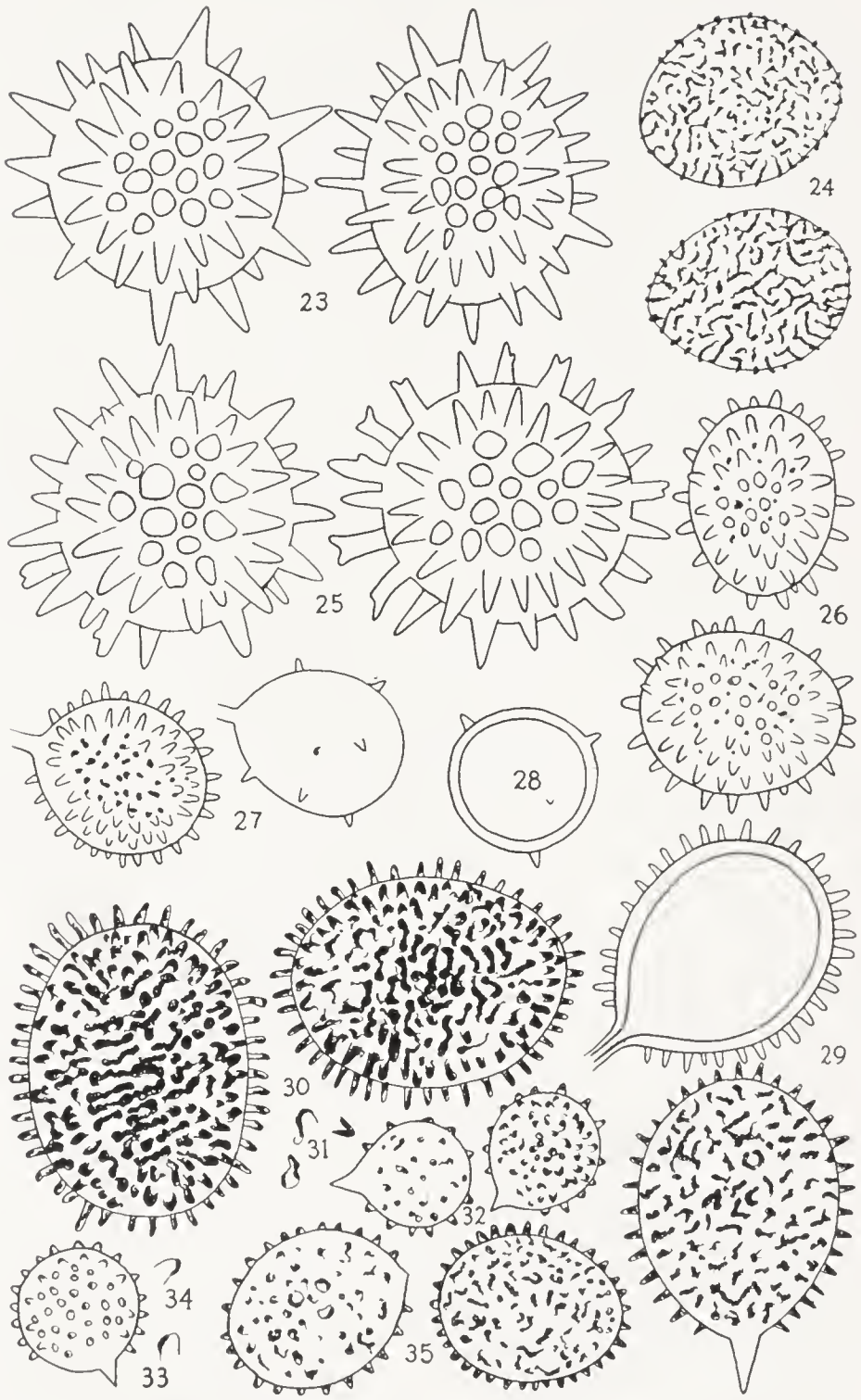

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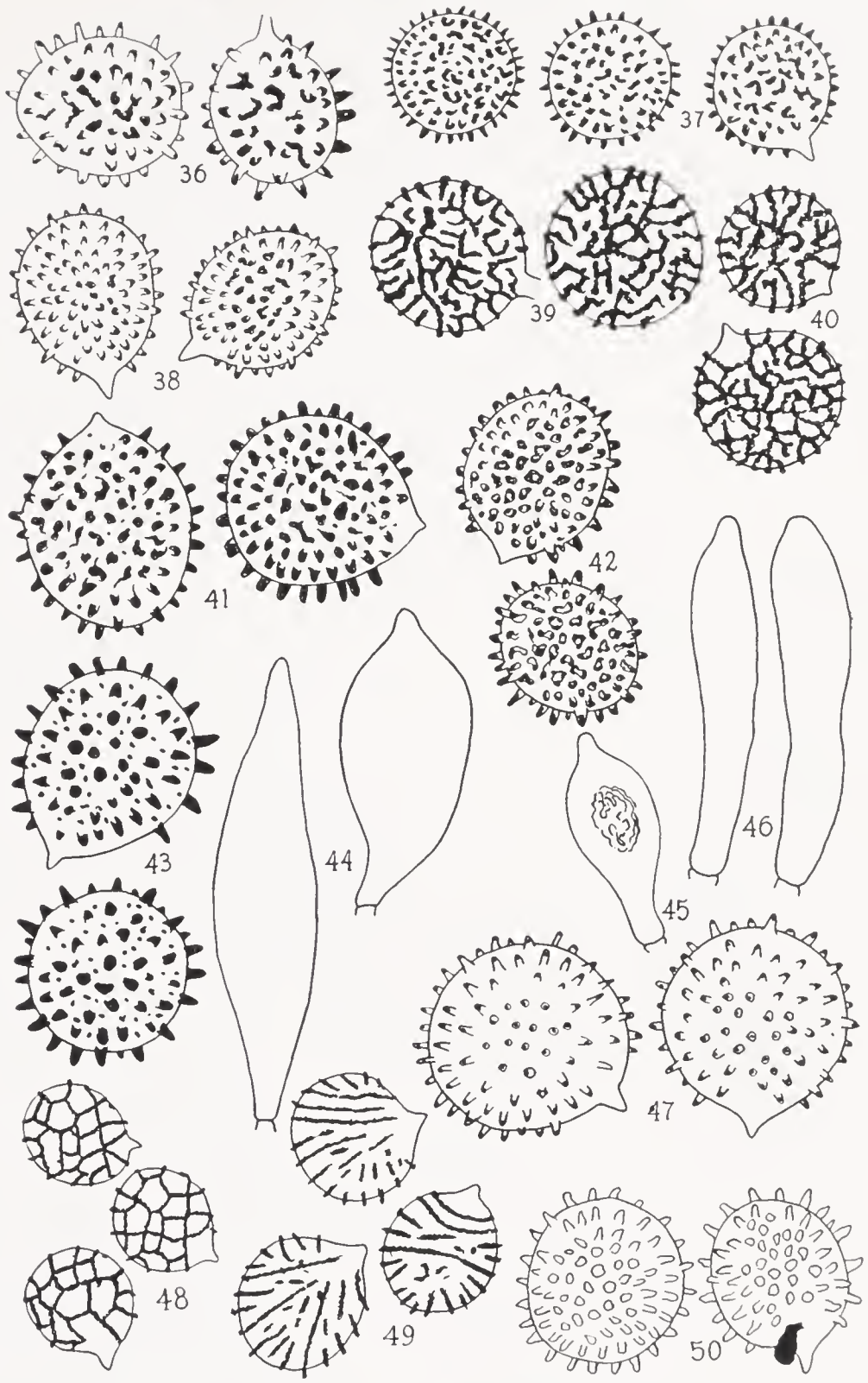

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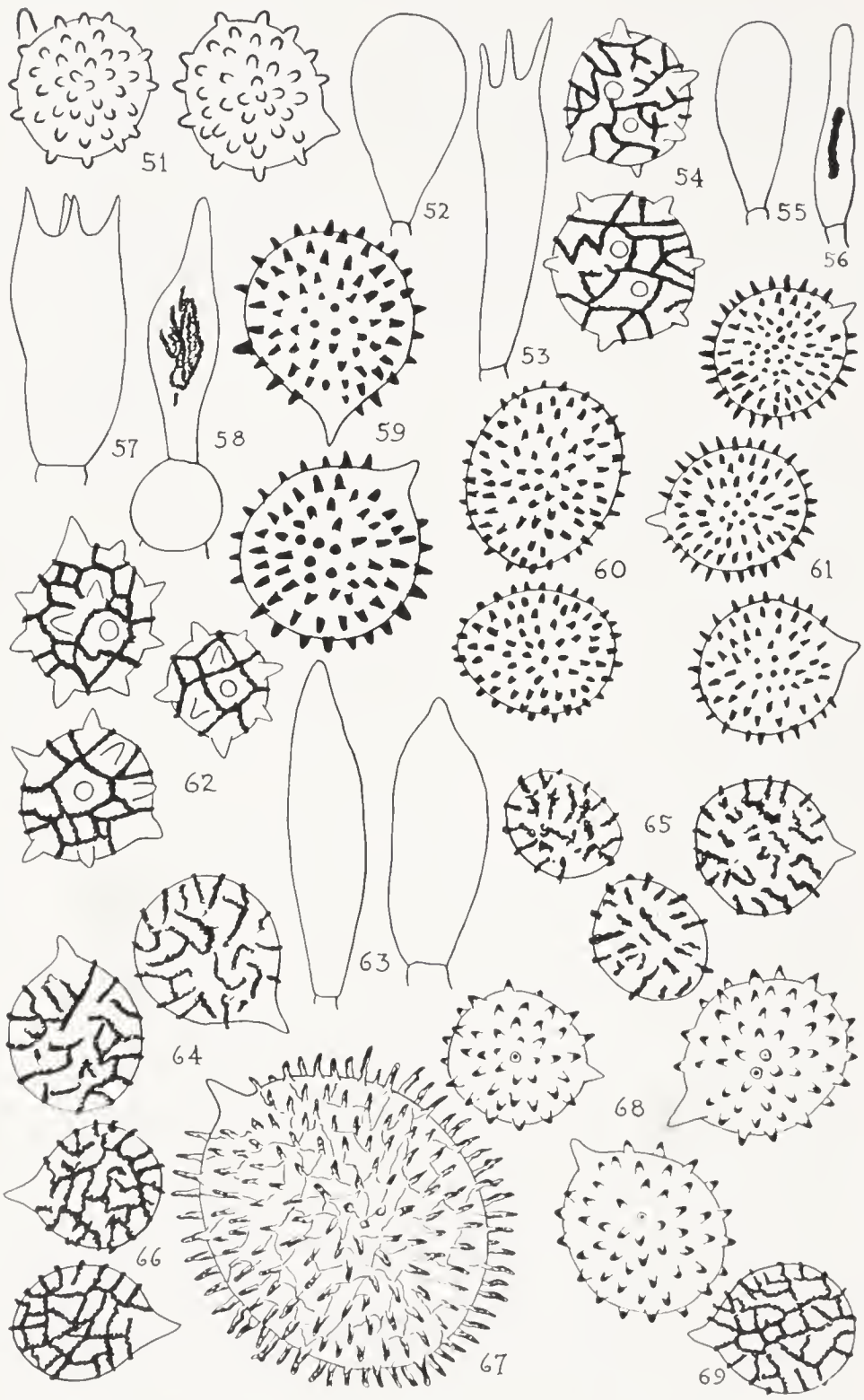

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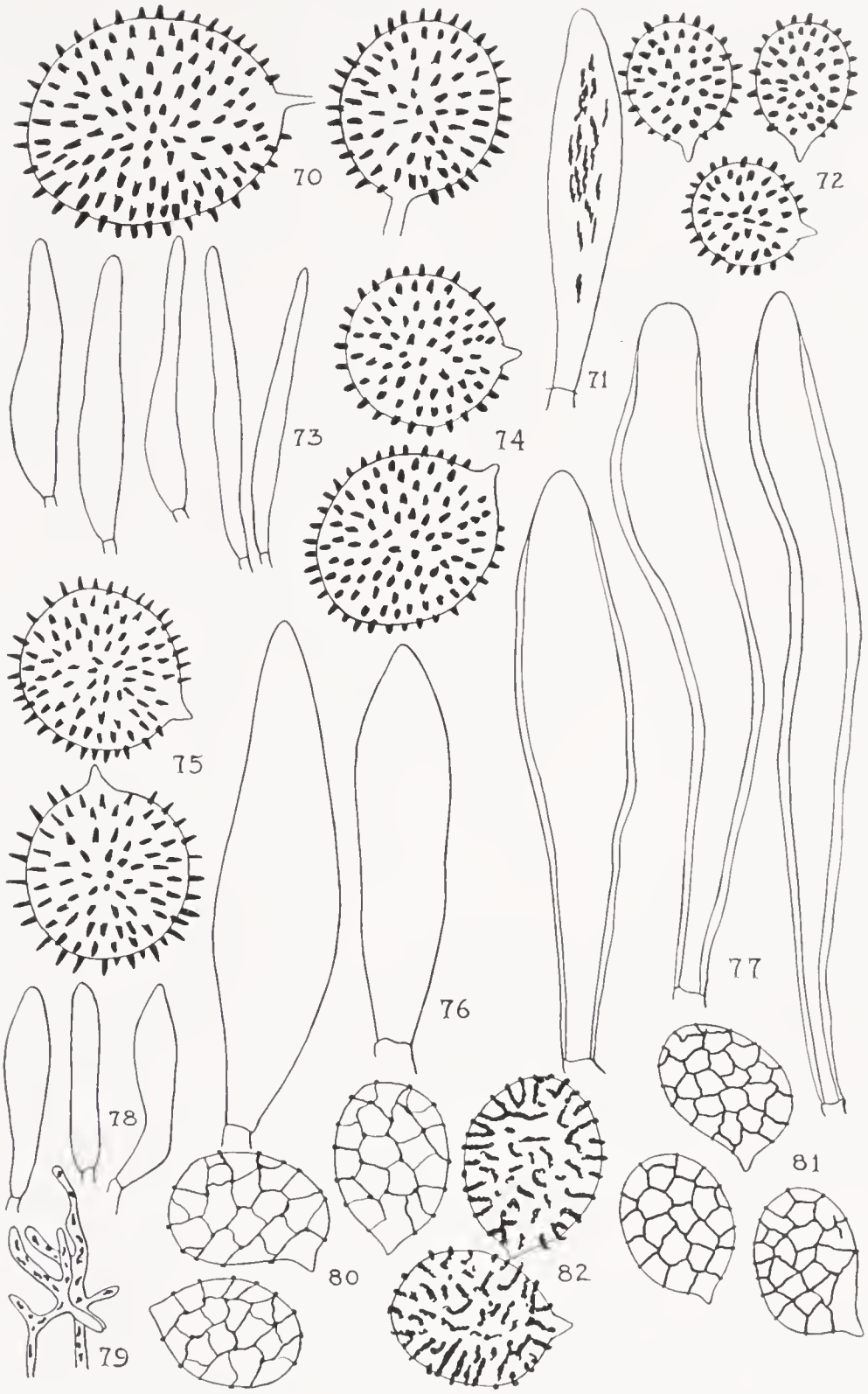

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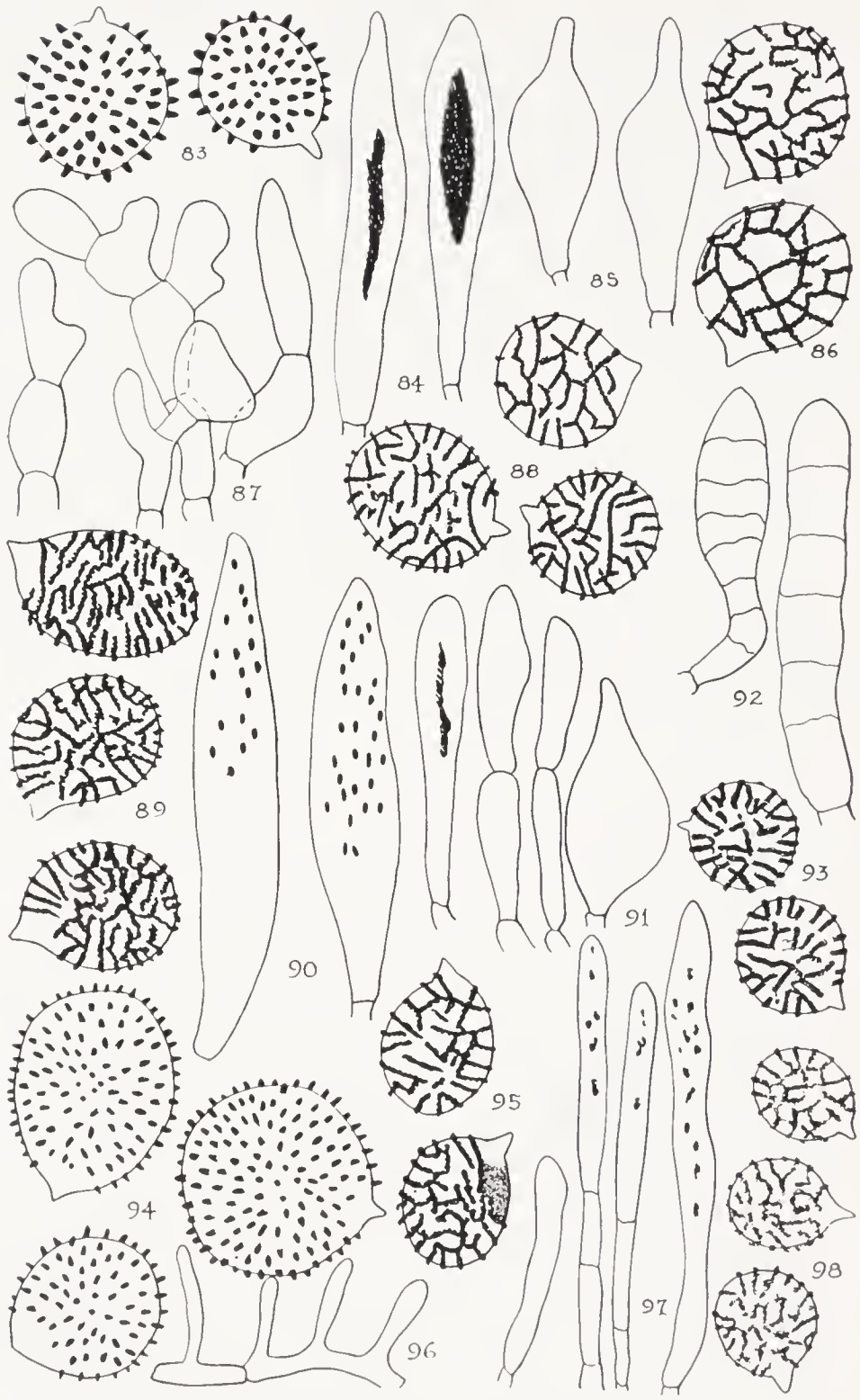

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Memoirs
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The Torrey Botanical Club

Vol. 21, No. 4 **January 10, 1963**

Editor
MURRAY F. BUELL

A MONOGRAPHIC STUDY OF THE FERN GENUS CYSTOPTERIS

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Published for the Club by
THE SEEMAN PRINTERY
Durham, N. C.

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INTRODUCTION

The apparent differences in the form of sori have been in many cases the basis for referring species of *Cystopteris* to other genera. For example, before it was recognized as a distinct genus in 1806, Linnaeus in his *Species Plantarum* (1753) had included two species in the genus *Polypodium* because of the round sorus. Smith (1793) included *Cystopteris fragilis* in *Cyathea* because its bladder indusia resembled the globose indusium of his new genus. Others, including Bernhardi (1802) who referred *Cystopteris bulbifera* to *Cyathea*, continued this practice. Swartz (1801) included three *Cystopteris* species in his genus *Aspidium* which was later construed in various ways making it a mixture of diverse elements.

Bernhardi (1806) was the first to recognize the characteristic indusium and its position of attachment to the receptacle. As a result he created the genus *Cystopteris* and transferred *Aspidium fragile*, *montanum* and *bulbiferum* to it.

In the comprehensive work *Tentamen Pteridographiae* by Presl (1836) *Cystopteris* was maintained as a distinct genus and was placed in section *Cystopterideae* of the tribe *Aspleniaceae*. This designation reflected the globose, laterally attached indusium.

Hooker, in his *Genera Filicum* (1842) followed Presl's treatment, placing *Cystopteris* near genera such as *Acrophorus* and *Leucostegia* based on the indusial position. This relationship was again indicated in Hooker's *Species Filicum* (1846).

The next major change in the expression of generic relationships of *Cystopteris* was that of Christ (1897) who placed this genus with *Hypoderris*, *Woodsia* and others in the family *Aspidiaceae*. Diels (1902) essentially followed this same treatment.

The concept of Bower (1928) in regard to *Cystopteris* relationships was that this genus is near the Cyatheoid derivatives, namely the Woodsioid and Dryopteroid ferns. Christensen (1938) placed *Cystopteris* with *Athyrium* in the subfamily *Asplenioideae*. Ching (1940) followed this same concept by placing *Cystopteris* in his family *Aspleniaceae*, tribe *Athyricae*.

The most modern comprehensive treatise on fern genera is that of Copeland (1947). He places *Cystopteris* within the largest of his families, the *Aspidiaceae*, which includes such genera as *Athyrium*, *Dryopteris* and *Woodsia*.

A more recent classification by Holttum (1949) places *Cystopteris* in the subfamily *Athyrioideae* of his diverse family *Dennstaedtiaceae*. He believed that there is evidence that these elements arose from a primitive type resembling *Dennstaedtia* but have now become widely divergent.

The postulation of generic relationships is probably beyond the scope of this study, which deals exclusively with the infrageneric categories of *Cystopteris*. However, in studying the apparently primitive members of the genus, it becomes apparent that there are similarities with other genera, primarily *Athyrium, Dryopteris* and to a lesser extent *Woodsia*.

The initial plan of this investigation was merely to study the widely variable *Cystopteris fragilis* in an attempt to evaluate whether it is one species or, in fact, a group of superficially similar species. Early in the study, however, it became evident that there are apparently several distinct species; and that the variability of *C. fragilis* is due in part to intergradation and presumed hybridization between rather similar, although recognizable, species. Consequently, it seemed necessary to expand this investigation to cover the entire genus *Cystopteris* in all parts of the world. Some 5,000 specimens were examined altogether; and extensive anatomical studies, primarily with stained clearings of the pinnae, were undertaken to compare technical features of the indusium, laminar hairs, and epidermis of the different taxa. In addition, gametophyte cultures were made; and cytological observations were obtained from living plants procured in diverse areas of the globe. New studies of spore size and spore architecture revealed interesting and pertinent additional facts. A considerable mass of new data was thus brought to bear on the solution of problems in this genus. As a result of these new data, some rather major revisions of the taxonomy of *Cystopteris* had to be made.

In this treatment of the genus *Cystopteris* two subgenera are recognized for the first time, namely subgenus *Cystopteris* and subgenus *Acystopteris*. This subdivision has been made necessary because of the inclusion of two species from eastern Asia which are distinct in most of the diagnostic characters but which have in common with other species of *Cystopteris* two basic features. The subgenus *Cystopteris* has been subdivided into two sections, *Cystopteris* and *Emarginatae* in order to separate two postulated evolutionary lines within the genus. Two binomials have been omitted from this treatment because of the lack of authentic specimens, namely *Cystopteris tasmanica* Hooker and *C. mairei* Brause. *Cystopteris tasmanica* may very well be identical with *C. fragilis* var. *apiiformis* of this treatment. The original description of *C. mairei* indicates a close similarity with *C. sudetica* var. *moupinensis*.

Both herbarium specimens and living plants were studied during this investigation. Herbarium specimens were obtained from nine herbaria. In addition about one hundred and twenty-five living specimens were obtained in the United States and from various parts of the world.

As an important part of this investigation dealt with the anatomy of the pinna, the clearing technique of Foster (1949) was used to great advantage.

After the clearing process was completed, the pinnae were placed temporarily in a Clorox solution to remove any remaining coloration. Following rinsing in water they were ready for staining. The stain which was used exclusively with the pinnae was the ferric chloride-tannic acid stain of Foster (1934). This procedure was modified to the extent of substituting 50% alcohol solutions for aqueous solutions. This change appeared to give a more even stain to the tissues. While most of the pinna anatomy could be observed on the intact pinna, there were occasions when the indusia could not be induced to lie flat. In such cases it was necessary to dissect individual sori from the pinna and to mount them on a slide.

The gametophyte cultures were grown on sterilized soil in pots. They were kept at room temperature in a moist chamber and were placed near a north-facing window. Spores for studying the early stages of germination were grown on the surface of Modified Knop's Solution (Bold 1936).

The cytological material for the determination of chromosome number at meiosis was obtained from plants which were grown at the University of Michigan Botanical Gardens under relatively uniform conditions. Very young fertile fronds were placed directly into Newcomer's Fixative (Newcomer and Brant 1954). The contents of several sori were placed in a drop of acetocarmine and after covering with a coverslip, the squash technique was applied (Manton 1950).

All drawings, with the exception of spore and chromosome figures, were made with the aid of a microprojector. The spore and chromosome figures were traced by camera lucida. The silhouettes of leaves were obtained by following the technique outlined by Manton (1950).

MORPHOLOGY AND ANATOMY

The application of technical details of morphology, anatomy and cytology to the taxonomy and systematics of ferns has been a relatively new innovation. As recently as the 1920's the great bulk of taxonomic treatments dealing with this group were strictly on the basis of gross morphology. To be sure, there had been papers before this time which dealt with isolated morphological and anatomical problems. One example of this type of work is the series of papers on bulblets which appeared at the end of the nineteenth century. Matouschek (1894), Rostowzew (1894), Stevens (1898), Heinricher (1896, 1899, 1900) and Palisa (1900) all studied the morphologically interesting bulblets which are a means of vegetative reproduction in *Cystopteris bulbifera*. These papers, however, deal primarily with developmental and experimental morphology, and do not attempt to discuss taxonomic implications.

The first comprehensive work in which other disciplines were utilized in a taxonomic treatment of ferns was that of Bower (1923-28) in which detailed anatomy and morpology was applied. Ths type of approach has been continued recently with amplifications in various generic treatments, for example Wagner (1952) on *Diellia*, Brown (1958) on *Woodsia*, Tryon (1957) on *Pellaea* and Kramer (1957) on *Lindsaea*.

Spores

The spores of *Cystopteris* have been studied by several workers in attempts to determine whether the spines which are characteristic of most of the species are associated with the exospore or with a perisporial covering. Luerssen (1889) merely referred to the spines as being associated with the exospore. Hannig (1911), McVaugh (1935) and Christensen (1938) have indicated that the spores lack a perispore, thus supporting the view that the spines are part of the exospore. The opposite view is taken by Selling (1946) who, in working with the Hawaiian species *Cystopteris douglasii*, found that "the spiny sculpture seems to be part of a perisporial covering." Indeed his figure of the spore, which was prepared by the acetolysis method, which commonly removes the perispore, shows the spines to be lacking.

In an attempt to resolve this apparent difference of opinion, spore samples of four species were prepared by the acetolysis method. A sample of *Cystopteris* × *alpina* spores, which have the architecture characteristic of the majority of *Cystopteris* species, retained the spines after treatment, as did also *C. douglasii*. *Cystopteris japonica* spores also retained their characteristic architecture. On the other hand, a sample of the rugose spore type from *C. fragilis* shows a smooth exospore on which is superimposed a layer which gives the rugose architecture typical of this variety. However, as this outer layer was not removed by the acetolysis technique, one must assume that it may not be a perisporial layer but in fact an integral part of the exospore.

There are three distinct types of exospore architecture within the genus *Cystopteris*. The condition common to the majority of species is that of the echinate spore. The extreme examples of this type are found in the *C. fragilis* complex and *C. diaphana* where the spines are long-attenuate with acute apices (Plate 15, fig. J). Other species such as *C. bulbifera*, *C. montana* and *C. sudetica* possess spores which have a tendency toward shorter spines with the apices of these spines being more rounded (Plate 15, fig. E).

The second type of spore architecture is that which differentiates the plant formerly treated as *Cystopteris dickieana* (but here treated as a

form not worthy of taxonomic designation) from *C. fragilis*. This is the rugose spore (Pl. 15, fig. Q) which resembles closely the spores found in such genera as *Athyrium, Dryopteris* and *Woodsia*. It might be appropriate here to suggest the possibility that this spore type may have been possessed by the stock which gave rise to the above genera and *Cystopteris* and is now only of limited occurrence in *Cystopteris*. It is interesting to note that in occasional specimens of *C. montana* the spores approach the rugose condition though they do not duplicate it exactly.

Also, Hagenah (1961), in his extensive studies on the "dickieana" spore type in North America, finds that there is a rather complete transition series between the rugose and the echinate spore within the *C. fragilis* populations. I likewise have found intermediates both in the United States and Europe. Thus, while most specimens may be identified with the respective spore form, there are some populations which become problematical.

The third spore type is found in the subgenus *Acystopteris*. This group of two species is different from the rest of the genus in several respects, of which the architecture of its spores is very distinctive. The projections of the spore are not approximately cylindrical as in subgenus *Cystopteris* but are highly irregular as seen in cross-sectional outline (Pl. 15, fig. F-H).

All three spore types are bilateral and monolete. The shape of the spores is somewhat variable, ranging, depending on the view, from oval to the more general "bean-shaped" outline.

An "average" spore size is not obtainable for the majority of *Cystopteris* species. The reason for the variation is primarily the presence of polyploid series with variations in chromosome number which results in changes in spore size. This phenomenon is treated in the portion of this paper dealing with chromosomes and spore-size.

Gametophyte

The fresh spores of *Cystopteris* require approximately three weeks to germinate. This period, however, may be as much as two weeks longer when older spores are utilized. Viability decreases as the spore age increases and spores over one year old have a very low germination percentage.

The germination of *Cystopteris* gametophytes is very similar to that described for other leptosporangiate ferns, e.g. *Diellia* (Wagner, 1952) and *Woodsia* (Brown, 1958). The exospore cracks open near the central region of the spore in an irregular manner exposing the protoplast which is crowded with chloroplasts. Soon after the exposure of the protoplast, a rhizoid is produced as an extension of the cell wall (Pl. 16, fig. A, B). In fact, two rhizoids have been observed on the initial cell before any further

development of the gametophyte occurs. These rhizoids are unicellular and lack chloroplasts. Under what are assumed to be normal growing conditions (northern exposure and lack of crowding) the cells of the filamentous stage number from two to four with the cells remaining a roughly oval shape. This stage may, however, produce a much extended series of elongate cells under crowded conditions.

Subsequently the lateral expansion of the prothallus is attained by the formation of a longitudinal wall in the terminal cell by lateral divisions of an apical cell and by the creation of an apical meristem (Pl. 16, fig. H-M) similar to that described by Stokey (1951).

The mature gametophytes resemble closely those typical of the higher leptosporangiate ferns (Pl. 17, fig. A). The outline is roughly cordate with broad wings extending to either side of the apical notch. The prothallus is only one cell thick with the exception of the archegonial cushion which is two or three cells thick. The superficial cells and (more commonly) the marginal cells may possess unicellular hairs of the papillate type as described previously by Stokey (op. cit.).

Gametophyte cultures of five species (*Cystopteris fragilis, C. douglasii, C. protrusa, C. diaphana* and *C. bulbifera*) and two putative hybrids (*C.* × *alpina* and *C.* × *tennesscensis*) have been grown in an attempt to find specific differences within the gametophyte generation and to determine whether apogamy occurs. All of the taxa examined are similar in the bulk of their gametophytic features and none were apogamous.

There is one aspect of *Cystopteris* gametophyte morphology however which has yielded differences, but as only a few species and populations have been cultured, no definite conclusions can be made as yet. The differences which have been observed concern the abundance and position of papillate hairs on the prothallus. Within the *Cystopteris fragilis* complex (*C. fragilis* and *C. douglasii*) these hairs arise relatively late in the development of the prothallus and they are very sparse (Pl. 17, fig. E). They have not been observed on superficial cells, and appear to be limited to the marginal cells. The marginal cells on which the hairs occur give a smooth outline to the prothallus.

On the other hand, the culture of *Cystopteris diaphana* shows that the hairs appear soon after the cell plate stage is initiated and they are more numerous, being primarily on the marginal cells but occurring also on some superficial cells. The marginal cells do not give a smooth outline to the prothallus and the marginal hairs are most commonly superimposed on cells which extend outward from the main mass of the prothallus (Pl. 17, fig. D) thus forming a rather irregular outline. The hairs are also somewhat longer and narrower than those in the *C. fragilis* complex. A similar distribution of hairs has been observed in the gametophyte of *C.* ×

alpina (which is intermediate between *C. fragilis* and *C. montana* and is presumed to be their hybrid) although the features of the margin are not as striking as that in *C. diaphana*. It might be justified to postulate then that *C. montana* has a gametophyte trichome orientation similar to that of *C. diaphana* though this fact is yet to be determined experimentally.

The sex organs of *Cystopteris* have not been examined critically as they appear to have developmental patterns similar to those of the majority of higher homosporous leptosporangiate ferns. The antheridia originate on the ventral surface among the rhizoids before the archegonial cushion is completely developed. They mature about four to five weeks after spore germination under normal growing conditions and are fully developed well before the archegonia are receptive to sperm. Gametophytes may thus be entirely antheridial when young. This condition may also result from crowded culture conditions or from the reduction in the amount of light available to the prothallus as stated by Stokey (1951). Schlumberger (1911) reported that *C. fragilis* and *C. montana* possess antheridia with undivided cap cells only, unlike the related *Woodsia* and other genera in which the cap consists of two cells.

Under the conditions of culture used in my work the archegonia appear approximately six weeks after spore germination on the ventral surface of the archegonial cushion just below the apical notch. Within six weeks after the appearance of archegonia, sporophytic development is evident providing there has been an adequate water film available so that sperms could swim to the archegonia. This film was created by flooding the culture dishes with water after both sex organs were mature.

The Young Sporophyte

The initial stages of sporophyte development in *Cystopteris* are essentially the same in those species which were observed, namely *C. bulbifera*, *C. fragilis* and *C.* × *tennesseensis*. The following discussion of the developmental sequence in *C.* × *tennesseensis* may therefore be applied in a general manner to that of the other species in the subgenus *Cystopteris*. The sporophytic development in the subgenus *Acystopteris* has not been examined to my knowledge.

The first evidence of embryonic activity is the appearance of a protuberance on the ventral surface of the prothallus in the cushion region. The first frond emerges and grows toward the notch between the prothallial lobes. At the same time the first root appears and grows toward the base of the prothallus though its growth is soon directed toward the substrate.

The first frond has a twin-lobed blade with dichotomous venation (Pl. 18, fig. A). (The difference in vein position relative to the margin, which

distinguishes section *Cystopteris* from section *Emarginatae,* appears on the earliest leaf stages in my cultures of *C. fragilis* and *C.* × *tennesseensis.*) The stipe is heavily clothed with hairs of two types, the multicellular glandular hair and the unicellular glandular hair (Pl. 9, fig. E 2, 3). The multicellular glandular hair type is more abundant toward the base of the stipe and becomes sparse to lacking toward the blade. Occasionally these hairs have superimposed on them the unicellular hair type and may result in a rather complex branched hair (Pl. 9, fig. E 6). The unicellular glandular hair is prevalent throughout the length of the stipe and is widely distributed on both the superficial and marginal cells of the blade. For the most part this hair type is unicellular although occasionally there are two-celled transitional hairs. True scales are entirely lacking on the stipe of the initial frond and, in fact, do not appear until the development of the fourth or fifth frond.

The succeeding steps of the heteroblastic series of leaves (Pl. 18) show the usual transitions to a pinnately organized blade. The apparent overtopping of a vein and expansion of the lamina within one of the two blade lobes results in a three-lobed blade. Subsequent overtopping in sequence gives rise to the pinnate condition common to the genus *Cystopteris.*

The Mature Sporophyte

Root. The roots of the genus *Cystopteris* are fibrous and originate singly at a position on the rhizome which is below the attachment region of each stipe. Numerous very narrow lateral branch roots are borne along the main root axis. The roots of four species (*C. sudetica, protrusa, bulbifera, japonica*) have been examined superficially in order to detect differences, if present, in their anatomy but were found to be very similar in their cross-sectional plan. The outline of the cross section is circular, although the stele is somewhat elliptical. The outer three or four layers of cortical cells are rather heavily sclerified though not totally occluded. The stele is diarch with a group of protoxylem elements at each end of the elliptical stele. The bulk of the xylem is composed of two large metaxylem elements in the species examined with the exception of *C. japonica* in which there were four conspicuous metaxylem elements. This discrepancy may, however, be due to the fact that the roots of this species are more robust and thus have a greater diameter.

Rhizome. The rhizomes of species of the genus *Cystopteris* are primarily wide-creeping, with the exception of *C. fragilis* and *C. bulbifera* where the internodes are very short and the rhizome is essentially sub-erect. The rhizome internodal length of the wide-creeping species varies greatly. In the case of *C. montana, C. sudetica* and its Asiatic derivatives the internodal

length is considerable, being from one to three and one-half centimeters. The rhizome of these species ranges up to two millimeters in diameter and has a cord-like aspect. On the other hand, the rhizome of *C. bulbifera* is so thickly beset with stipe-bases that it is only by removing them that the true extent of the rhizome proper may be observed. *Cystopteris protrusa*, *C. douglasii* and *C. japonica* are intermediate in internodal length and have a more robust rhizome, that of *C. japonica* having a diameter of six to eight millimeters or greater.

The internal anatomy of the *Cystopteris* rhizome has been summarized by Ogura (1938). He places the genus with a group of others, including *Woodsia*, *Dryopteris*, *Athyrium* and *Asplenium*, which have in common the possession of a radially arranged true dictyostele. This organization is found in plants with erect as well as creeping stems.

The rhizomes of *C. japonica*, *C. sudetica*, *C. protrusa*, *C. bulbifera* and the apparent introgressant *C. diaphana* × *fragilis* (traditionally referred to as *C. fragilis* var. *mackayi*) have been examined during the course of this study. In the first three species the radial dictyostele is clearly discernible because the internode distance is relatively great. However, in *C. bulbifera* and to a lesser extent in *C. diaphana* × *fragilis* a radially organized dictyostele is rarely observed in its entirety because of the short internodes with resultant increase in the number of leaves arising in any given section.

A series of rhizome cross sections have been examined for the species *Cystopteris protrusa* in order to examine the mature anatomy. The cross section of the rhizome proper is roughly a triangle with rounded points, its greatest dimension being between two and three millimeters, depending on its age. The outermost two or three layers of cells are rather heavily sclerified. Within this sclerified layer lies a rather uniform parenchyma ground tissue in which the stelar bundles are arranged radially. The stele is approximately 1.0 mm. in diameter and shows three stelar bundles. The meristeles are oval in outline, being 0.25-0.35 mm. broad and 0.14-0.20 mm. wide.

The dictyostele of *C. protrusa* was dissected out of such a rhizome (by treatment in sodium hydroxide and subsequent boiling) and the gaps were observed to be 1.3-1.8 cm. in length. Near the median position of each gap a double trace arises, one from each side of the gap, and extends into the frond. At the base of the gap arises the trace of the root which accompanies each frond.

Scales of Rhizome and Stipe. The scales which invest the rhizome and basal stipe region in *Cystopteris* differ rather markedly in the various species groups. Primarily they are ovate-lanceolate on the rhizome and become progressively more linear-lanceolate as they extend up the stipe.

The stipe scales show various degrees of cell-wall thickening. Rather thick-walled and sometimes completely occluded cells occur in such species as *C. fragilis*, *C. douglasii*, and *C. bulbifera*. In *C. sudetica* and its Asian relative *C. pellucida* the lateral walls have become uniformly thickened and thus these scales have attained the elathrate condition (Pl. 7, fig. G) which is a distinctive characteristic of several fern families including *Aspleniaceae* and *Vittariaceae*. On the other hand, scales of *C. protrusa* and *C. montana* show relatively little lateral-wall thickening.

The presence of glands on the scales is a rather widespread phenomenon within the genus *Cystopteris* and is considered by the present author to be the primitive condition. The unicellular glands are primarily marginal although superficial glands have occasionally been observed. Glands are present on scales of both species within the subgenus *Acystopteris*. They are also universally present in *C. montana* and *C. sudetica* var. *sudetica*. The Asian relatives of *C. sudetica*, namely *C. sudetica* var. *moupinensis* and *C. pellucida*, have scales without glands. In *C. diaphana* the European and African specimens are generally glandular and this condition is carried over to the scales. However, the Central and South American plants more frequently are eglandular although some glandular specimens have been observed from this region. No members of the complex strictly centering around *C. fragilis* (*C. protrusa*, *C. fragilis*, *C. douglasii*) have been observed to possess glandular scales.

In certain collections, structures intermediate between scales and hairs have been observed in the lower rachis region (Pl. 7, fig. E 4). However they are sporadic and do not seem to be constant for any given species.

The Leaf and its Parts. *Leaf Axis.* The stipe itself does not possess any distinctive features in the various species of *Cystopteris* other than pigmentation, average diameter, and length relative to the blade. These features have been utilized in the segregation of species. A dark almost ebony pigment has apparently evolved separately in two distinctly different *Cystopteris* groups and this condition is considered to be the advanced or derived condition. *Cystopteris japonica* in the subgenus *Acystopteris* possesses this feature which immediately separates it from the other Asiatic species, *C. tenuisecta*, with its stramineous stipes. This pigmentation does not appear until the frond is almost completely expanded. It then advances upward from the base of the stipe and in about fifteen days is characteristic not only of the stipe but also of the rachis and the major axes of the pinnae.

The only other species in which this dark pigmentation occurs is *Cystopteris fragilis*. The distribution of this condition geographically is somewhat sporadic, however, and may be due in part to environmental conditions. It has been observed in plants from northwestern India, eastern Africa,

Europe, along the Andean mountain chain in South America and in Central America. The stipe color in the majority of *C. fragilis* specimens examined by me has been the stramineous or light tan coloration which is characteristic of the remaining species within the genus.

All members of the genus *Cystopteris* possess stipes which are adaxially sulcate. The stipe length ranges from 2.5 centimeters in Alaskan specimens of *C. fragilis* to about 45 centimeters in *C. tenuisecta*. The basal stipe diameter ranges from 0.5 millimeters in some *C. fragilis* specimens to 5.0 millimeters and greater in the Asiatic *C. tenuisecta*.

The relative length of the stipe as compared with that of the blade is rather distinctive in certain of the species. *Cystopteris montana* and *C. sudetica* have stipes which may be as much as two or three times as long as the blade. At the other extreme are *C. fragilis* and *C. diaphana* in which the stipe are almost universally shorter than the blade.

In his treatment of the vegetative anatomy of the pteridophytes, Ogura (1938) describes the internal anatomy of the *Cystopteris* stipe. He stated that the stele consists of two meristeles whose abaxial ends unite with each other in the stipe or in the rachis, so that the stele here forms a V-shape in cross section. Both xylem ends of each meristele are curved into hooks.

The region of the stipe at which the two bundles unit has been used by Shaver (1949) as a character to segregate species. He finds that the bundles are free throughout the stipe in *C. fragilis* and *C. bulbifera* while they are united into a flattened V in *C. protrusa*. So far as I have been able to determine, however, comparable fronds from different species are essentially alike. This character is rather hazardous to use in separating species because the stelar condition fluctuates greatly according to the size of the leaf. Thus a juvenile type of frond of *C. bulbifera* has been observed to have the two bundles united a full one and one-quarter inches below the basal pinna. Cross sections of the stipe of a sterile adult-type frond of *C. sudetica* show the bundles to be free throughout, finally joining in the rachis one-quarter inch above the basal pinna.

In addition to scales which are primarily limited to the rhizome and basal stipe region, three other structures may be present on the frond axis of *Cystopteris*, namely multicellular non-glandular hairs, uni- and multicellular glandular hairs, and vegetative propagules or bulblets.

The multicellular non-glandular hairs are confined, in this genus, to the subgenus *Acystopteris*. Being relatively large, these hairs are visible without magnification. They occur primarily on the frond axes (the rachis, pinna axis and along veins) although they do arise also superficially on both laminar surfaces. The number of cells making up the hair range from seven to twelve (Pl. 10, fig. E).

The unicellular glandular hair is very prevalent on the rachis and minor axes of glandular species of *Cystopteris* and thus is rather widespread in the genus (Pl. 11, fig. E 2-4). Occasionally unicellular hairs are superimposed on the multicellular glandular hairs. Their abundance on individual plants, however, varies considerably and there may commonly be only one or two multicellular glands on a given pinna. The other extreme is that in which the rachis is rather heavily beset with these glands and this led Milde (1867) to place plants possessing this condition in a distinct variety, *C. fragilis* var. *huteri*.

Vegetative propagules occur within the genus *Cystopteris* only in *C. bulbifera*. The stage in origin and development of these propagules has been described in detail by Rostowzew (1894). These "bulblets" occur abaxially primarily near the attachment region of the upper pinnae with the rachis. They sometimes arise, however, on axes of the pinnae. The bulblets are composed of two green fleshy "cotyledons" between which, after the bulblets fall in an appropriate spot, a new sporophyte plant arises. These young plants assume mature features very rapidly and one has been observed in which the first frond (measuring 8.0 mm.) already possesses four sori. The bulblets of *C. bulbifera* are typically glabrous (well illustrated by Geske, 1925) but may also possess a few scales and they abscise readily from the parent frond. However, the apparent hybrids of *C. bulbifera* with *C. protrusa* and *C. fragilis* produce bulblets which remain firmly attached to the frond at maturity. Furthermore they may be covered with dark scales. They are also more or less irregular in form and Wagner and Hagenah (1956) report that there is a tendency for sporangia to occur around the sides and base of the hybrid bulblets.

Much experimental work has been undertaken with vegetative regeneration in the genus *Cystopteris*. This research has probably been stimulated in part by the presence of bulblets in *C. bulbifera*. Heinricher (1896) studied the effects of drying on the bulblets and (1900) reported having obtained the development of adventitious buds on isolated basal parts of the fronds of *C. montana*, *C. fragilis* and *C. alpina*. He also demonstrated that the isolated so-called "cotyledons" of bulblets of *C. bulbifera* will give rise to adventitious buds. Palisa (1900) demonstrated that these buds, whose position is not predetermined, arise from the proliferations of epidermal cells. Lawton (1936) has studied regeneration phenomena in *C. fragilis*.

General Blade Pattern. There are two blade patterns represented within the genus *Cystopteris*. The deltoid outline results from the fact that the basal pinnae are longer than the subsequent pinnae. This frond plan is characteristic of the whole subgenus *Acystopteris* (Pl. 10, fig. A) and the subgenus *Cystopteris* section *Emarginatae* with the exception of *C. dia-*

phana. In addition, it is found in *C. protrusa* and *C. douglasii*. *Cystopteris bulbifera* possesses a modification of this plan in which the apex of the frond is greatly attenuated. The lanceolate plan results when the basal pinnae are shorter than the pinnae directly above them. This plan is represented by *C. diaphana* and *C. fragilis* (Pl. 2, fig. A).

The blade of *Cystopteris* ranges in length from 2.5 cm. in *C. fragilis* to 50 cm. in *C. tenuisecta* and these two species also represent the extremes in blade width.

Pinnation and Venation. The extent of blade dissection varies somewhat even among individual species of *Cystopteris*. Thus *C. fragilis* forms occurring in Alaska, are once-pinnate whereas specimens from Greece may be delicately cut and tripinnate. Specimens of *C. tenuisecta* may be as much as quadripinnatifid (Pl. 11, fig. A).

The range in number of pinna pairs per frond is even more striking within the genus. Mature fronds of *C. fragilis* may have as few as seven pinna pairs whereas *C. bulbifera*, with its attenuate frond, may have as many as 30 or more pairs (Pl. 8, fig. A). The pinnae may be subopposite or alternate on the same frond. The pinnules are arranged anadromically on the pinnae throughout the genus without exception.

The veins within the pinnules are free and branch in an approximately dichotomous manner. In all members of the genus *Cystopteris* with one exception, the elongate epidermal cells which are superimposed on the veins extend to the cells that make up the pinna margin (Pl. 9, fig. C). The exception is found in the southern hemisphere populations of *Cystopteris fragilis* which inhabit New Zealand, the extreme southern tip of South America, the Falkland Islands and South Georgia. In these regions the elongate epidermal cells stop two or three cells short of the margin and normally lobed cells are intercalated between them and the marginal cells. This latter condition resembles very closely that which Brown (1958) reported as being characteristic of the entire genus *Woodsia*.

The position of the vein endings at the margin of the pinna has been found to be extremely important in species descriptions and in the expression of species relationships within the genus *Cystopteris*. In the majority of the species the veins are directed into conspicuous emarginations (Pl. 8, fig. C). This phenomenon is very precise and does not deviate within a species! However, one section of the genus, including *C. protrusa* and *C. fragilis*, has veins which (with rare exceptions) run into the tips of marginal teeth (Pl. 2, fig. C 1-2). The vein endings in subgenus *Acystopteris* are more difficult to interpret in this manner since the lobes of the pinnae are rounded instead of having definite teeth (Pl. 10, fig. C) but they are apparently intermediate in this character.

Laminar Anatomy. Features of the laminar anatomy of *Cystopteris*, namely the epidermis and occurrence of hairs, have been investigated critically in an attempt to find characters of specific distinction. Of these the characteristic patterns of the adaxial epidermal cells were found to be most rewarding. The subject of hair types has been considered in the section dealing with the leaf axis.

Within the subgenus *Cystopteris* there are two distinct upper epidermal cell outlines which may be used to distinguish two very much confused species. *Cystopteris diaphana* has epidermal cells which possess smooth or merely undulating outlines (Pl. 9, fig. B 2). This is in marked contrast to the condition in *C. fragilis* where the upper epidermal cells have outlines reminiscent of pieces in a jigsaw puzzle (Pl. 2, fig. B 2 and 4). Introgressant populations involving these two species show varying degrees of intermediacy in their cell outline. The other members of section *Cystopteris* also possess these lobed epidermal cells. The remaining members of the subgenus show intermediacy in the degree of epidermal cell lobing (Pl. 8, fig. B 2).

The subgenus *Acystopteris* is characterized by the fact that the epidermal cells are on a much more diminutive scale (Pl. 10, fig. 2 and 4) than in plants with corresponding polyploid levels in the subgenus *Cystopteris*. Correlated with this reduction in epidermal cell size is the reduction in guard cell size.

The stomata occur exclusively on the abaxial laminar surface. They vary greatly in size depending on their position, those near the veins and along the margins tending to be smaller than those in the intervenal areas. There is some correlation between polyploidy and stomatal size. The plants with high polyploid levels (Pl. 2, fig. B 1) tend to have larger stomata than the diploid plants (Pl. 8, fig. B 1).

The marginal cells of the lamina are rather uniform throughout the genus *Cystopteris*. They present a rather jagged circumference (Pl. 9, fig. C), when viewed under magnification, similar to that found in some species of *Woodsia* (as illustrated by Brown, 1958). This is a totally different aspect from the species of *Athyrium* (a genus believed to be closely related) which have been examined where the marginal cells are so uniform that one cannot determine, by observing merely the edge of the pinna, where one cell ends and the next one begins.

The Sorus. The development of the sorus in *Cystopteris* has been studied by Goebel (1915) and Bower (1928) among other workers. Goebel, in studying an early stage of the sorus in *C. montana*, found as follows:

> Angelegt wird die Placenta—deren Entwicklung nicht lückenlos verfolgt wurde—entweder aus dem Blattrand oder in dessen nächster Nähe auf der Blattunterseite, auf der auch bald das Indusium hervorsprosst.

> Die Entwicklung (oder Weiterentwicklung) des Blattrandes wird aber zunächst gehemmt, während die Placenta ziemlich stark anschwillt, tritt der letztere kaum hervor, erst später nimmt er sein Wachstum auf und schiebt dann den Sorus ausgesprocken auf die Unterseite.

Thus Goebel finds the sorus to be essentially a marginal sorus which is later forced to the lower surface by marginal growth. Bower, who studied the young leaf margin of *C. fragilis*, also found the young sorus in close proximity to the margin. He further states: "The facts of development of the sorus in *Cystopteris* thus show a near similarity to those seen in *Lindsaya*, which is held to be a Davallioid derivative: in fact a marginal type." No further studies of soral ontogeny in *Cystopteris* have been made since the studies of Bower.

The fully developed sorus of *Cystopteris* is clearly superficial, however, and is a mixed sorus. It is inserted abaxially and is dorsal on a vein which then continues to the margin of the pinnule. The indusium is attached at the basal portion of the receptacle nearest the pinnule axis and forms a hood which covers the young sporangia. It is free toward the pinnule margin (Pl. 11, fig. D).

The extent of indusial attachment to the base of the receptacle varies within the genus. In *C. fragilis* the attachment region may cover only one-third of the receptacular circumference (Pl. 2, fig. D) while *C. bulbifera* and *C. pellucida*, with their very broad indusia, may extend about two-thirds the distance (Pl. 6, fig. D).

Indusial size, though relatively constant for a given species, differs within the genus. *Cystopteris japonica* possesses such a minute indusium that its protective function, if any, can be available only during the initial developmental stages of the sorus. Indeed, the mature sporangia must be removed in order to observe the indusium (Pl. 10, fig. D). *Cystopteris protrusa* possesses a very delicate and frequently fugacious indusium. In the remaining species, on the other hand, the indusium is more readily evident at all stages of maturity.

The shape of indusial cells aids materially in clarifying the taxonomic elements which have been relegated, in the past, to *Cystopteris fragilis*. An examination of indusial cells of *C. fragilis* shows very narrow linear cells with a rather orderly arrangement. As the sorus matures, mechanical breakage occurs along the longitudinal walls of the cells, especially at the indusium apex. This breakage results in the lacerate indusium which has frequently been described as typical of the species (Pl. 2, fig. D). The *C. diaphana* indusium, on the other hand, is composed of shorter and broader cells, and there appears to be very little tendency for splitting of the indusial apex, so that a relatively entire indusium results (Pl. 9, fig. D).

Cystopteris fragilis and *C. douglasii* have frequently been observed to

possess accessory hairs attached toward the base of the indusium's outer surface. There may be one or more hairs present (Pl. 2 and 4, fig. D). Once a well organized structure resembling a miniature indusium was observed in place of these hairs. This may well have phylogentic significance since both species are in the section *Cystopteris*. Such hairs have not been observed in *C. protrusa* or in any other members of the genus.

Glandularity of the indusium is widespread within the genus *Cystopteris* and is considered to be the primitive condition. However, the glandular condition has evidentally been lost secondarily in all evolutionary lines. Species within section *Cystopteris* have not been observed to possess glandular indusia with the exception of a local form of *C. fragilis* on Kerguelen Island in the southern part of the Indian Ocean. However, hybrids and introgressant specimens involving *C. fragilis* may possess glandular indusia. In section *Emarginatae*, *Cystopteris pellucida* and *C. sudetica* var. *moupinensis* lack glandular indusia as does *C. japonica* in subgenus *Acystopteris*.

The sporangium of *Cystopteris* consists of a stalk and capsule and is representative of Aspidioid ferns in general. The stalk is composed of three tiers of cells. The tier below the capsule is three cells wide but the subsequent tiers are reduced to two cells. The stalk is well-developed throughout the genus with one exception. *Cystopteris diaphana* has been observed to possess very short stalks so that the mature capsules may appear to be almost sessile. By dissecting out the sporangia, however, it may be seen that the three tiers of cells are present but that they are very much compressed. The annulus is interrupted and an average of 13-16 thickened cells has been determined for the genus. However, in individual specimens, averages of from 10 to 21 cells have been observed.

CHROMOSOMES AND SPORE SIZE

The study of fern cytology was given great impetus by the pioneering work of Manton (1950). She treated the major cytological phenomena arising in the Pteridophyta with numerous examples to supplement her discussion. It was the difficulty which confronted her while studying the genus *Cystopteris* cytologically that led her to the application of the squash technique to the higher ferns. She states:

> The introduction of the squash method resolved the technical impasse at once, but thereby revealed a cytogenetic problem of quite unusual complexity, a circumstance which was nevertheless to be expected in view of the well-known taxonomic confusion prevailing in the genus.

Manton treated three European members of *Cystopteris* in her initial work, and found two different chromosome numbers represented, namely n = 84 and n = 126. The European *C. fragilis* was found to have both these numbers while *C. montana* possessed the lower number. *Cystopteris alpina* (which is discussed in more detail below in the section on "Hybridization") was found to have the number n = 126. This evidence led Manton to postulate the presence of a polyploid series within the genus *Cystopteris* and to predict the probable occurrence of a lower level in the series:

> The relationship between numbers as different as 126 and 84 may not at first leap to the eye, yet we can hardly doubt that we are dealing with the upper members of a polyploid series, the lower ones of which are still to seek. If a form with a gametic number of 42 could be found we should have a simple series of 42, 84 and 126 in which the plant bearing them would be diploid, tetraploid and hexaploid respectively.

The next cytological work in the genus *Cystopteris* was the report of Britton (1953) of a diploid species (n = 42), namely *C. bulbifera*. This established 42 as the basic chromosome number for the genus. Other chromosome counts for the genus are also given in this publication. This was followed shortly by the discovery (Wagner and Hagenah 1956a) that the taxon known to American botanists as *C. fragilis* var. *protrusa* is also a diploid. To add to the broad cytological picture of the genus, I have found that *C. douglasii*, the Hawaiian segregate of *C. fragilis*, has a chromosome number of n = ca. 168 thus making it an octaploid.

Table 1 lists chromosome numbers which have been obtained from the *Cystopteris* collections which were grown by the author in the University of Michigan Botanical Gardens, including those for three new taxa. Voucher specimens are deposited in the University of Michigan Herbarium. Representative photographs and explanatory diagrams of these chromosome counts are found on Plates 20-22. The earlier reports (Wagner 1955) of chromosomes of "*C. fragilis* var. *tennesseensis*" from Michigan refer to *C.* × *laurentiana;* and those of "*C. fragilis* var. *simulans*" from Pennsylvania and Maryland refer to *C.* × *tennesseensis.*

Other evidence points to the fact that there are polyploid series within other species of *Cystopteris*, although perhaps not as complete as that within the *C. fragilis* complex. Mr. Dale J. Hagenah (Cranbrook Institute of Science, Bloomfield Hills, Michigan) has studied the North American species of *Cystopteris* rather extensively in order to find if there is any distinct correlation between spore size and the polyploid level of a plant. He has found (Hagenah 1961) that the average spore size of a plant within this genus indicates with great accuracy its polyploid level. His technique is to make measurements at random of ten normal spores on a spore slide.

TABLE 1. *Chromosome observations.*

Species	Chromosome Number
	n
Cystopteris japonica Luerssen	
Oku-musashi, Saitama Pref., Central Honshu, Japan. (*S. Kurata*, coll.)	42
C. diaphana (Bory) Blasdell	
a. Agua del Palo, 1000 meters elev., Santiago, Prov. Chile. (*P. Valenzuela and F. Vergara*)	42
b. Chicua, 2750 m. altitude, Irazu Volcano, Costa Rica. (*J. Leon*)	126
C. protrusa (Weatherby) Blasdell	
a. Gold Hill, Taos Co., New Mexico. (*E. F. Castetter 9596*)	42
b. Dream Haven Cottage, near Wonderland Hotel, Elkmont, Tennessee. (*H. H. Vannorsdall*)	42
C. fragilis (L.) Bernh.	
a. Slopes near the coast of Nahuel-Huapi-Lake, 780m. elev., Peninsula Quetrihue, Parque Nacional de Nahuel-Huapi, Provincia Neuguen, Argentina. (*J. Diem*)	84
b. Germany. (*H. Merxmüller*)	84
c. Yates Center, Woodson Co., Kansas. (*R. L. MeGregor*)	84
d. Italy. (*E. Ehrendorfer*)	ca. 126
e. Eastern Alps, Austria. (*E. Ehrendorfer*)	126
f. France	ca. 126
g. Canterai San Blas, Cuzco, Peru. (*C. Vargas*)	ca. 126
h. Simmons Woods near Duel Lake, Mackinac Co., Mich. (*R. Blasdell 198*)	84
C. douglasii Hook.	
Puulaau, on west slopes of Mauna Kea, alt. 7600 ft., Hawaii. (*E. Horner*)	ca. 168
C. X tennesseensis Shaver	
a. 0.9 mi. W of R 26 and 69 intersection on R 69, at base of rock outcrops along road, Fairfield Co., Ohio. (*R. Blasdell 230*)	84
b. ½ mi. SW of Fort Washington, Montgomery Co., Pa. (*E. T. Wherry*)	84
c. Catoctin Furnace, Frederick Co., Md. (*E. T. Wherry*)	84
C. X laurentiana (Weatherby) Blasdell	
2 mi. W of Deer Lake, near Ishpeming, Marquette Co., Mich. (*R. Blasdell 194*)	126

He then averages these measurements and arrives at a size which corresponds closely with the spore size which is characteristic of one of the polyploid levels. One random sampling is sufficient to determine the chromosome number in a great majority of cases. Occasionally, however, I have found that an average spore size will lie on the border line between two polyploid levels. In such a case, an additional random sampling will place the plant in the correct category. Table 2 gives the size ranges (in microns) of each polyploid level in the genus *Cystopteris* and also the approximate averages, as determined by the present author.

It should be noted that the spore size ranges of certain levels overlap. However, the average spore size is characteristic of a given polyploid level. It was, in fact, the observance by Hagenah of two spore sizes in the Michigan terrestrial populations of *C. fragilis* complex that ultimately led to the discovery by Wagner of the diploid member.

Thus we have a tool for determining from herbarium specimens the

TABLE 2. *Polyploid level correlation with spore size.*

Polyploid Level	Spore Size Range (in microns)	Average Spore Size (in microns)
2x	27 - 32	ca. 29
4x	32 - 42	ca. 36
6x	38 - 48	ca. 43
8x	43 - 53	ca. 48

approximate geographical ranges of polyploid levels within individual species. These data are valuable, among other things, for more accurate assignment of putative parents to hybrids as will be shown in the section on hybridization.

I have used the character of spore size rather extensively in an attempt to ascertain the extent of polyploid development within each species of *Cystopteris*. Table 3, though probably incomplete, does show several

TABLE 3. *Polyploid levels within the genus Cystopteris as indicated by spore size.*

Species	2n	4n	6n	8n
C. tenuisecta	X	—	—	—
C. japonica	X*	X	—	—
C. protrusa	X*	—	—	—
C. fragilis	—	X*	X*	X
C. douglasii	—	—	—	X*
C. diaphana	X*	X	X*	—
C. montana	X	X*	—	—
C. sudetica	X	—	—	—
C. pellucida	X	—	—	—
C. bulbifera	X*	—	—	—

* Indicates polyploid levels in which the chromosome number has actually been determined.

interesting features within the genus. First, the diploid condition is apparently extant in all the species groups, in the *C. fragilis* complex being represented by *C. protrusa*. Second, the most completely developed polyploid series are found in the species with more primitive characteristics (described below in the section on species relationships) and/or the wider ranges. This development is very likely correlated with a greater age of these elements, thus providing more time for the evolution of such a series.

A cursory examination of spore size distribution within the genus indicates that the diploid populations are, in the main, restricted in their distribution while the polyploids have much more extensive ranges. Of the diploids, *C. protrusa* (in the *C. fragilis* complex) has the most limited range, occurring in its typical form almost entirely in the Appalachian and Smoky Mountains of the eastern United States. Its apparent range

is greatly extended by introgressant populations into which the genetic material of the southern hemisphere *C. diaphana* has apparently been introduced. Another diploid, *C. bulbifera*, is confined to southeastern Canada and the eastern two-thirds of the United States. Small-spored collections of *C. montana* have been observed from both Canada and Europe but the great majority of collections represent the tetraploid level. *Cystopteris sudetica* and its Asian variety *moupinensis* have uniformly small diploid-sized spores. Thus it is probably the widest ranging diploid species in the genus, extending from Bavaria to Shensi and Szechuan provinces in China. (I have available only ten collections of this species from Russia and Asia so that the distribution data is very scattered.) *Cystopteris pellucida*, a relative of *C. sudetica* and endemic to China, also has small spores.

The polyploid populations of *C. fragilis* increase in abundance the further north they occur. As has already been mentioned, the diploid *C. protrusa*, along with introgressant populations, is prevalent in the eastern United States. The tetraploid *C. fragilis* with its variety *mackayi* (the latter here interpreted as a result of *C. diaphana* introgression) form the bulk of the populations in northern United States and in Canada. Hexaploids, though less frequent, are also present in this region. A similar pattern occurs in Europe, and there tetraploids and hexaploids are apparently present in approximately equal numbers. The lack of diploid populations of the *C. fragilis* complex in Europe may well be attributed to the extensive glaciation which has occurred in that region. It is in the far north, particularly Alaska and northern Canada, that populations yielding extremely large spores become more prevalent. These spores are equivalent in size to those of *C. douglasii*, the Hawaiian endemic in which the octaploid level has been determined. Thus it may be assumed that these subarctic plants are in fact octaploids. These extremely large spores found in the northern latitudes have, for the most part, the rugose architecture which is characteristic of a common variant of *C. fragilis*. However, a few collections have also been found in which the large spores have the echinate architecture of typical *C. fragilis*.

The importance of polyploidy in the flora of northern and high altitude regions has been presented by several workers. Tischler (1935) presented the cytological information dealing with the flora of Schleswig-Holstein. He found that, of the species which extend northward, sixty percent are polyploid. On the other hand, the species extending southward are only twenty-seven percent polyploids. Flovik (1940), in reporting the polyploid situation in the flora of Spitzbergen, stated that eighty percent of the species are polyploid. Cain (1944) in discussing the problem of polyploidy comments:

> Flovik interprets these figures as evidence of a tendency toward the fact that increased chromosome number increases adaptability to extreme habitats, such as arctic and alpine conditions, and that polyploidy appears to have played an important role in the origin of forms which have been able to colonize cold regions.

This is probably the correct explanation for the distribution of polyploidy in *Cystopteris* in the northern hemisphere.

HYBRIDIZATION

The subject of hybridization is of great importance in a study of the genus *Cystopteris* for it is in the attempt to classify plants of this probable origin that much confusion has resulted in the past. Hybrids have generally been referred to the species which they most closely resemble and have been named thus as either varieties or forms. Inclusion of these plants with those typical of the various species has naturally tended to a wider extension of the apparent diversity of the individual species and to obscure their real nature. Thus it becomes necessary to segregate these hybrid elements from the parental species and to give them distinct designations.

There are three general phenomena which seem to have had a profound influence on the evolutionary trends within the genus *Cystopteris*. They are (1) autopolyploidy, (2) introgression, and (3) allopolyploidy. As autopolyploidy has been considered in some detail in the section on chromosomes, only brief mention of it will be made here as necessary.

Introgressive Hybridization

The concept of introgressive hybridization has become widely accepted in the last two decades and new species of organisms, both plant and, to a lesser extent, animal, are constantly being reported in which this phenomenon occurs. Anderson (1949, 1953) and Stebbins (1950) have discussed it in some detail. Introgression results from the hybridization of two closely related species in a region where the two species overlap in their ranges. The offspring may or may not be partially sterile depending on the genetic similarity of the two parental genomes. The point is that whatever fertility is present tends to form a bridge between the species over which genetic characteristics of one species can be transmitted into the population of the second species. Thus as Stebbins (1950) has stated:

> Introgressive hybridization, whatever may be its importance in modifying and amplifying the variation pattern of certain individual species, is nevertheless by its very nature not a way of producing new morphological or physiological characteristics, and therefore of pro-

gressive evolution. It merely produces convergence between previously more distinct species.

There is strong evidence of introgressive hybridization within the "*Cystopteris fragilis* complex." This group has been methodically sidestepped by taxonomists in the past who have simply lumped together all populations which superficially resembled *C. fragilis*.

The most obvious character which separates non-introgressant *Cystopteris fragilis* and its related species from the rest of the genus is the extension of its veins into teeth at the pinna margin. If this criterion were used for species distinction, however, one would be obliged to rule out a large segment of the traditional *C. fragilis* sensu lato in which all the veins extend into depressions at the pinna margin. Litardière (1912), among other European botanists, has recognized this distinction in anatomy by setting up a subspecies *C. fragilis* ssp. *diaphana* (Bory) Litard. for the latter condition.

I believe that we are dealing here with two distinct species. Not only are the vein terminations different, but there are two additional anatomical characters which support this contention, namely (1) the shapes of the upper epidermal cells, and (2) the outlines of the indusial cells. The upper epidermal cells of *Cystopteris fragilis* are deeply lobed (Pl. 2, fig. B 2) while those of *C. diaphana* are rather uniformly straight-walled or merely undulating (Pl. 9, B 2). Introgressant populations possess varying degrees of epidermal cell lobing showing intermediacy between the two parental species. The indusial cells of *Cystopteris fragilis* are long and relatively narrow (Pl. 2, fig. D). Toward maturity the indusium frequently becomes lacerate at the apex. Much of this is apparently due to separation along the length of the cells as the sorus develops since the young indusia I have examined are relatively entire. *Cystopteris diaphana*, on the other hand, possesses indusia with shorter and relatively broader cells; the indusium remains relatively entire in the later stages and encircles the receptacle more broadly. In addition, other differentiating features, namely the development of sporangial stalks and the margin of the gametophytes, have been described in the section dealing with morphology. Thus, in indusial as well as other anatomical characters, *C. diaphana* resembles more closely the condition found in the rest of the subgenus *Cystopteris* even though it is superficially similar to *C. fragilis*.

Cystopteris fragilis and *C. diaphana* have their own distinct geographic ranges in which the above anatomical characters correlate for the most part, but there are intermediates to be found, especially where their ranges overlap or come in close proximity. In these areas the populations become difficult to identify. This situation results from the fact that these plants are intermediate in their diagnostic characteristics. The correlation of

species characters thus breaks down in the regions of overlap and diverse combinations result, and occasional intermediate specimens are found even at some distance from the actual zones of geographical proximity.

The most probable explanation for these intermediate populations is that gene flow takes place freely between *Cystopteris fragilis* and *C. diaphana* where their gametophytes are growing in close proximity. A close genetic relationship of these two species is suggested by the fact that there is no apparent reduction in the fertility of the intergrades.

The presence of *Cystopteris* intergrades, in areas distant from the overlapping region of the putative parents, may well be a point of serious concern to those who have observed and studied introgression within the flowering plants. However, until introgression is better understood in homosporous plants, intermediate populations within the flowering plants should not be stereotyped and used as a model to be applied to introgression within other large plant groups. The reason for this objection is primarily mechanical as an examination of the respective life cycles will indicate.

The seed of the angiosperms is, in general, a relatively heavy, substantial structure. Thus it would, in the main, drop to the ground soon after release from the ovary. As a result, the introgressant population might perhaps expand slowly at the periphery of the overlap area while still maintaining a continuum through which backcrossing could occur repeatedly.

The dissemination propagule (spore) of the ferns presents a totally different aspect which could result in an entirely different distribution pattern. The spore of *Cystopteris* is relatively small (ca. 30-50 μ) and maintains its viability up to a year or more. The populations of *Cystopteris* in the overlap zones of *C. fragilis* and *C. diaphana* are essentially montane (e.g. Mexico, Canary Islands, eastern Africa, etc.) which would increase the ease with which the spores could be introduced into the prevailing air currents. Thus spores produced by intermediate individuals in the overlap region could be disseminated to distant areas rather easily depending on the whims of atmospheric movements. These spores might (or might not) eventually produce large intermediate populations at a great distance from the original introgressive region. This concept would explain the frequent sporadic occurrences of *C. diaphana* and *C. diaphana* × *fragilis* beyond their expected ranges. The latter taxon, for example, is represented by the plant, currently known as *C. fragilis* var. *mackayi*, which presents a uniform morphology throughout the eastern and midwestern United States.

The condition in the "*Cystopteris fragilis* complex," therefore, is not necessarily the result of "worldwide introgression" as might be concluded from a cursory examination of the distribution map (Pl. 23). It could be

equally well the result of the dissemination of spores which were produced by intermediate individuals in the region of overlap.

A question logically follows an acceptance of such a hypothesis. Has there been any subsequent mixing of genetic material between these disjunct intermediate populations and those of the prevalent parent in the region? This question will probably not be answered with any degree of assurance until extensive hybridization experiments are carried out between populations of "pure" *Cystopteris diaphana* and *C. fragilis* to test the degree of similarity in their respective genomes. It is conceivable that the arctic populations of *C. fragilis* in the interior of North America and Asia, for example, may be sufficiently distinct, due to their apparent isolation from the *C. diaphana* element, to result in sterile hybrids when crossed. Such a line of investigation would, of course, have to be based on hybridization between parents with the same chromosome number as polyploid series are present within these two taxa.

Allopolyploidy

The occurrence of hybrids involving species of *Cystopteris* with genetically distinct genomes has been implied or partially demonstrated by several botanical investigators in the past. At least one of these reports is very dubious.[1] A very likely interspecific hybrid in the genus *Cystopteris* has been described by Christ (1900) based on a collection by Shuttleworth at Creux du Van (in the Jura Mountains of western Switzerland) in August 1834. His evidence, though based entirely on gross morphology, does show an intermediacy between *C. fragilis* and *C. montana*. A detailed discussion of this hybrid appears in the section dealing with the taxonomy of the genus.

Weatherby (1926) described *Cystopteris fragilis* var. *laurentiana* as a large member of the species. Although he did not ascribe hybrid origin to it, he did allude to its greater size and blunt pinnules, "characters which, Prof. Fernald states, give it in the field the aspect of a *C. bulbifera* without the long apex of the frond."

[1] Parmentier (1900) published an account of an apparent hybrid between *Cystopteris fragilis* and *Asplenium trichomanes* which he named *C. Blindi*. His evidence is entirely based on the anatomy and gross morphology of a sterile plant. The only morphological evidence which he cites to suggest *A. trichomanes* is the small pinna size. Anatomically, his evidence dealing with pinnae (mesophyll and epidermis) could apply to both *Cystopteris* and *Asplenium*. Perhaps the best case for hybridity in his investigation is the shape of the vascular strands in the petiole which apparently resembles that in *Asplenium*. However, his two figures illustrating this character may not be from comparable positions. The figure illustrating the *C. fragilis* condition has two separate traces while the one depicting *Asplenium* shows the traces already joined. Thus it is probably best, until the chromosome situation can be investigated, to consider this taxon merely as one of historical interest.

In 1944 Wherry published on a locality in Berks County, Pennsylvania where *Cystopteris protrusa* and *C. fragilis* var. *mackayi* grew at the base of a cliff. Farther up the cliff plants where found which possessed glandular indusia and occasionally bulblets, characters in common with *C. bulbifera*. When these plants were submitted to Dr. Weatherby for an opinion, he suggested hybridization between *C. bulbifera* and *C. fragilis*. An interesting feature of this locality was that *C. bulbifera* was not known to grow nearer than fifteen miles from this station. Wherry suggested that this might be another case similar to those mentioned by Wagner (1943) where spores from a remote source provide gametes to form a hybrid in a habitat where the incoming species could not exist.

Wagner (1944) reported another occurrence of this apparent hybrid *Cystopteris* at Catoctin Furnace, Frederick County, Maryland. Since these initial publications have made botanists aware of this hybrid combination, numerous localities have been reported.

Shaver (1950) described as a new species, *Cystopteris tennesseensis* and specified the putative parents as *Cystopteris fragilis* var. *protrusa* × *C. bulbifera*. He also listed several characters which showed the intermediate nature of this taxon between the two species. In the same year McGregor (1950) published on the diversity of this hybrid in the central United States, primarily Kansas and Missouri although he proposed a new combination *C. fragilis* var. *tennesseensis*. He regarded this variety "to be of hybrid origin but it now is a self-perpetuating plant which has become established over a considerable area." This conclusion was reached because of the absence of *C. bulbifera* over a large part of the hybrid range in Kansas and Missouri. He also elevated Weatherby's *C. fragilis* form *simulans* to the varietal level, and indicated its close relation to var. *tennesseensis* because of the occasional presence of bulblets.

The first cytological evidence on the *Cystopteris bulbifera* hybrids was contributed by Wagner (1955). He found that these populations segregated into two groups, those with a chromosome number of n = 84 and Michigan populations with n = 126. During the same year Hagenah (1955) reported finding the Michigan hybrid in four counties. However, he did not feel that these populations should be attributed to *C. tennesseensis* without further study. Wagner and Hagenah (1956b) reaffirmed their position that the Michigan populations are not identical with *Cystopteris tennesseensis* and suggested "that they may represent an undescribed taxon." I have found that the anatomical and morphological characters of the Michigan hybrids match those of *C. fragilis* var. *laurentiana* and have thus deemed it necessary to make the new combination, *C.* × *laurentiana*.

In extrapolating to parental taxa which would agree with the characteristics of these hybrids one can find species which fit them rather closely. In the case of *C.* × *tennesseensis* (n = 84) Shaver was evidently right in his selection of the parental species so far as my investigations can show. The chromosome numbers of both *C. bulbifera* (Britton 1953) and *C. protrusa* (Wagner & Hagenah 1956) have been established as n = 42. Since the chromosome complements of the parental genomes are balanced numerically, there appears to be a more or less equal distribution of parental characters in the hybrid.

Cystopteris × *laurentiana* (n = 126), on the other hand, leans toward one parent in the majority of characteristics. This phenomenon can be explained by analyzing the probable genome constitution of this hybrid. *Cystopteris bulbifera* (2n), of necessity, would be one parent (supplying among other characters the laminar propagules which occasionally occur on the hybrid). For the other parent, a tetraploid taxon would be required. There are two prime candidates which could probably have served as a parent of this hybrid: (1) *C. fragilis* and (2) the commonly cited and rather uniform *C. fragilis* var. *mackayi* (which I now believe to be a result of *C. diaphana* introgression).

Both putative parents are found throughout the range of *Cystopteris* × *laurentiana*. Characteristics in addition to bulblets which are indicative of *C. bulbifera* are the details of blade cutting, the somewhat tapered luxuriant frond, the sparsely glandular indusium. Trends toward *C. fragilis* are the increasingly incised pinnules, the linear cells comprising the indusium and the more irregularly lobed epidermal cells. Since the *C. fragilis* genome is represented twice whereas there is only one complement of *C. bulbifera*, it may well be assumed that the exaggeration of *C. fragilis* characteristics is due largely to the overbalance of *C. fragilis* chromosomes.

The abundance of these *Cystopteris bulbifera* hybrids as compared with other species hybrids within the genus is probably largely due to the fact that they possess, in the majority of specimens, a distinctive feature associating them with *C. bulbifera*, namely the vegetative propagule, the bulblet. It is definitely in the realm of possibility that most, if not all sympatric species within the subgenus *Cystopteris* hybridize among themselves where their ranges overlap. However, because of the subtle differences available to identify these hybrids, they are placed with one or the other parent. An example of this problem is the status of *Cystopteris* × *alpina* in Europe. This taxon has been treated, by European authors as either a subspecies (Luerssen 1889) or a variety (Milde 1867) of *C. fragilis*. Some have even treated *C. diaphana* as synonymous with *C. fragilis* ssp. *alpina*. This treatment is perhaps excusable as some forms of *C. diaphana* do resemble *C.* × *alpina* macroscopically.

Manton (1950) determined the chromosome number of *C. alpina* (from Switzerland) to be n = 126 (6X). I have measured spores from several European collections and find that they are regularly within the 6X size range. In order to decide what the putative parents of this hybrid were, there are two combinations of genomes which should be considered. It could be *C. fragilis* (2X) × *C. montana* (4X). This possibility should not be ruled out even though I have been unable to find a European collection of *C. fragilis* possessing spores within the diploid size range. However, this hybrid could have been formed at a time when the diploid *C. fragilis* existed in Europe and is now a fertile plant which is maintaining itself by spore reproduction. The other possible combination, which I favor, is that in which *C. fragilis* is the 4X parent with *C. montana* as the 2X parent. This would be the more probable cross because the European *C. fragilis* is primarily 4n or 6n while some *C. montana* collections have been studied which have spores of the 2n range. If this is, in fact, the correct parentage of *C.* × *alpina,* it is somewhat analogous to *C.* × *laurentiana* in that the characters of *C. fragilis* are expressed more completely in the hybrid than *C. montana.* The only apparent *C. montana* characters which are reflected in the hybrid are the cutting of the pinnules with veins mostly entering emarginations, and in the rather broad stipe scales. In all other respects it more resembles *C. fragilis.*

Another probable hybrid is *Cystopteris kausuana* which is known to me only from the type specimen. It possesses most of the macroscopic characteristics of *C. fragilis.* It also has rather long indusial cells which are indicative of this species. It differs, on the other hand, in the long, delicate stipe, the vein endings entering emarginations, and in the presence of clathrate scales. In these latter three features it resembles *C. sudetica* var. *moupinensis* and the other Asiatic derivatives of *C. sudetica.* It is impossible to postulate with any more certainty the exact origin of this taxon because the sori on the type specimen are immature and do not show the indusial and other structures at maturity. The few mature spores which were observed, however, were entirely aborted. Thus *C. kausuana* is very possibly a sterile hybrid in which chromosome doubling has not occurred.

GEOGRAPHICAL DISTRIBUTION AND HABITAT

The difficulty of obtaining critical data on habitats hampers the individual who tries to evaluate a group of plants primarily from herbarium specimens. The present study involves just such a situation for, with the exception of the author's field observations in the eastern United States,

information has been accumulated largely from floras covering varions geographic areas.

The members of the genus *Cystopteris* are primarily found in association with rock surfaces, either on rock faces, crevices, or on talus slopes. In Mackinac County, Michigan, *C. fragilis* has been observed growing on the sides of cracks in limestone pavement.

Wherry (1920) describes *Cystopteris fragilis* from a variety of situations such as "ledges of sandstone, schist and shale, as well as of limestone rocks, and also in talus and in woods entirely apart from any rocks." Typical *C. fragilis* appears to be limited almost entirely to epipetric situations. However, *C. protrusa*, of the eastern United States, which is closely related to *C. fragilis*, has never been reported growing on rock to my knowledge. It is found in rich woods with a loamy soil. *Cystopteris fragilis* var. *mackayi* (the apparent product of introgression between *C. fragilis* and *C. diaphana*) has a wider tolerance, growing on rocks as well as in soil. *Cystopteris douglasii* of Hawaii is also associated with rocks, growing in crevices and along the bases of cliffs.

Cystopteris bulbifera is more specific in its requirements, growing mostly in neutral soils associated with limestone. However, in Michigan it is found to grow luxuriantly in rich, moist *Thuja* swamps and in moist woods apparently with no contact with rock surfaces. *Cystopteris montana, C. sudetica* and its Asian derivative *C. pellucida* are apparently confined to epipetric situations. On herbarium labels the statement is repeatedly made that these plants were collected from rocks (calcareous rocks predominantly).

Little information is known to me concerning the habitat of *Cystopteris tenuiscula* and *C. japonica*. One herbarium label of the latter species states that the plant was growing in a beech forest. From this one might assume that it was not in association with rocks. Living material of this species has been received from Japan and the soil residue on the roots proved to have a pH of between 3.5 and 4.0. If this was the true pH in the natural habitat, it is by far the most acid condition encountered for the genus in this study, the remainder of the genus ranging from 6.0-8.0.

The genus *Cystopteris* is cosmopolitan in distribution although it is primarily restricted to temperate regions in the higher latitudes in both northern and southern hemispheres. However some mountain systems within the tropics possess sufficient altitude to produce temperate conditions and along these ranges the genus is well represented.

Cystopteris fragilis has the widest geographic range within the genus and is one of the few fern species which approach a cosmopolitan distribution. It attains its most wide-spread range in the boreal regions, extending through Europe and most of Asia and North America. Thus this species

is truly circumboreal. In addition, there are regions in the southern hemisphere where *C. fragilis* occurs quite disjunctly from its great northern range. New Zealand, Kerguelen Island (in the southern Indian Ocean) and the southern tip of South America possess populations with a very similar gross morphology. The closely related *C. douglasii* is endemic in the Hawaiian Islands.

Typical *Cystopteris protrusa*, with the deltoid blade plan, appears to be restricted to the Appalachian Mountain system, primarily in Tennessee and North Carolina. Toward the western and northern extent of its range (Missouri and Minnesota respectively) the blade plan becomes modified predominantly to the ovoid shape characteristic of *C. fragilis*. *Cystopteris bulbifera* presents a more ample distribution from Newfoundland to Manitoba and southward to Georgia and Arizona.

Cystopteris montana ranges strictly in the boreal regions. In the western hemisphere it is rather frequent in Canada and extends from Labrador to Alaska. The United States material of this species comes from two general regions. Glacier National Park, Montana, might be expected to harbor this species as the park is on the Canadian border. The other region is perhaps of more interest because of its apparently disjunct location. This is in the Sawatch Mountains of Colorado where it occurs at an altitude of about 10,000 feet. It is possible that there are intermediate localities in the mountains forming the Continental Divide which link this station with the bulk of the population in Canada. In Europe *C. montana* is widespread in the Scandanavian countries. It occurs in Scotland and is prevalent in the mountainous regions of central Europe. With the exception of a collection from Syktyvkar and one which may be from the Causasus, I have not seen this species from the USSR. It occurs in northwest India and in Kansu Province, China. Hooker (1868) states that it occurs also in Kamtchatka but no material has been available to me from this region.

Cystopteris sudetica is closely related to *C. montana* but has a more restricted distribution. It is most abundant in the mountains of Hungary and Czechoslovakia but also extends northwestward to Norway. To the east it occurs in the Caucasus Mountains and in western Russia. Its variety *moupinensis* has been collected in several provinces in central China. *Cystopteris pellucida* is restricted to central and eastern China but this apparent distribution is probably due to the paucity of collections.

Cystopteris diaphana, which in the past has been included in the polymorphous species *C. fragilis,* has an interesting disjunct distribution. Being present in its typical form (with glandular indusia) in the Canary Islands, Belgian Congo and northeastern Tanganyika Territory, this species is widespread from Mexico through South America in the mountain ranges.

Much of the New World material, however, lacks the indusial glands. This African-American distribution should not be surprising, however. As recently as 1958 Brown has stated: "One species, *Woodsia montevidensis*, occurs in the Drakensberg of Natal and in the Transvaal in South Africa. This species is also found in South America." Cain (1944) discusses this particular distribution using Steyermark's work (1932) on the genus *Menodora* as an example, among others. Cain continues:

> He [Steyermark] believes the most logical explanation to result from the postulation of a land bridge across the south Atlantic which was obliterated by the Upper Cretaceous. The geologists allow such a land connection (Devonian, through Jurassic to Upper Cretaceous), but the theory of continental displacement should be considered as a possibility along with the "lost continent" idea.

The members of the subgenus *Acystopteris* are confined to the southeastern region of Asia. *Cystopteris tenuisecta* ranges from northeast India south to Java and eastward through southern China to Honshu, Japan. The more restricted *C. japonica* occurs primarily in Japan but has been collected in Szechwan province, China.

A logical postlude to an analysis of distribution patterns within a group of organisms is to deduce a picture of the probable migration routes involved. This involves considering not merely distributional phenomena, however. The determination of the primitive elements and a correlation of their geography with that of the more specialized members of the group must be attempted.

There are two species groups which are candidates for being the primitive members (as analyzed in the section on species relationships) of the genus *Cystopteris*. Of these the subgenus *Acystopteris*, which includes *C. tenuisecta* and *C. japonica*, inhabits southeast Asia. *Cystopteris protrusa*, with its headquarters in the Appalachian Mountains of eastern United States, is the primitive element within the subgenus *Cystopteris* section *Cystopteris*. In its typical form it has the deltoid blade plan which is characteristic of the bulk of the genus. Such a disjunct distribution of the primitive elements is most easily explained by postulating that the genus *Cystopteris* evolved during the Carboniferous period when Gondwanaland presented an extensive land mass in the southern hemisphere. The subgenus *Acystopteris* probably became distinct early in the evolution of the genus. Initiated within the northeastern region of Gondwanaland, it later spread from northeastern India toward the east and south.

The progenitor of *C. protrusa* may also have followed an eastward route from north Gondwanaland and extended from eastern Asia to eastern North America. This hypothesis should not be very startling as it is well known that the floras of the two regions have many floristic elements in common.

Apparently the Appalachian Mountain system is the only remaining outpost for this ancestral stock. The section *Emarginatae* of subgenus *Cystopteris* probably evolved in northern Gondwanaland with the resulting elements taking two routes. The *C. montana-sudetica* element, with its present center in central Europe, very likely migrated through northwestern India toward the west. The other element, namely *C. diaphana,* established its extensive range in the central and western region of Gondwanaland.

Cystopteris fragilis very likely developed rather early from the progenitor of *C. protrusa* and had a wide geographic range in Gondwanaland. Subsequently the north temperate regions were added to the range of *C. fragilis* while the land mass of the "southern continent" was being reduced. All in all, the southern element of *C. fragilis*, now represented in Kerguelen Island, New Zealand, and the southern tip of South America, exhibits common features which are more primitive than its boreal counterpart.

SPECIES RELATIONSHIPS

In order to establish the probable relationships among the species of *Cystopteris* it has been necessary to assemble the data on morphology and anatomy which have been described in a previous section. These data are presented graphically by means of a chart containing concentric radii. The radii represent the total of specializations of the various species, and lines connect those species that possess characters in common. At certain points on the chart "missing links" are postulated in order to account for advanced tendencies common to certain species. Thus this diagram is based on the concept of the "common ground plan" (and it is adapted from a method developed by Dr. Warren H. Wagner, Jr. for his taxonomy courses at the University of Michigan).

In some of the characters selected for this presentation, the decision between primitive versus specialized conditions was obvious. In other characters, however, the tendencies were not clear and thus these characters had to be correlated with those possessing obvious trends. In still other characters no such correlation was possible and these are included on the chart merely to show similarities within species groups.

The twelve characters which were used in the demonstration of species relationships were selected because they either showed obvious trends and/or appeared to be stable in their expression within the various species. A table of specializations (Table 4) was constructed to show the evaluation of the primitive versus the derived condition of each character. The primitive condition was given a value of 0.0 while the derived expression of each

TABLE 4. *Specializations in Cystopteris.*

A. Rhizome long repent (0) to compact (1)
B. Blade pattern deltoid (0) to blade basally contracted (1)
C. Blade not apically attenuate (0) to attenuate (1)
D. Veins extending into marginal teeth (0) to veins into marginal depressions (1)
E. Undulating epidermal cell walls (0); shallow lobes (0.5); deep irregular lobes (1)
F. Cells of scales lacking secondary lateral cell walls (0) to thickened lateral cell walls (1)
G-H. Attenuate indusial cells (G) versus short cells (H)
I. Indusium glandular (0) to non-glandular (1)
J. Accessory indusial hairs absent (0) to present (1)
K. Foliar bulblets absent (0) to present (1)
L-M. Multicellular non-glandular hairs (L) versus multicellular glandular hairs (M)
N-P. Echinate spore (N); rugose (0); spines with highly dissected cross-sectional plan (P)

character received a value of 1.0. Intermediate expressions (where applicable) received a value of 0.5. These numbers were then totaled for each species and plotted on the chart. Thus *Cystopteris tenuisecta* with a total specialization of 1.0 would be considered the most primitive member of the genus while *C. fragilis* with a combined index of 5.0 ranks as the most divergent. The reasoning behind the evaluation of each of the twelve characters is summarized below:

A. RHIZOME HABIT. Within the genus *Cystopteris* the long repent rhizome with easily recognized internodes is the rule. In *C. fragilis* and to a lesser extent *C. bulbifera*, however, the stipe bases invest the rhizome so closely that the internodes may not be readily observed. This results from a more compact though still repent rhizome, and is considered to be a derived condition.

B. BLADE OUTLINE. The generalized outline for the genus *Cystopteris* is that of a broadly deltoid blade, i.e., with the basal pinnae the broadest However, two species, namely *C. fragilis* and *C. diaphana*, have evolved a more or less ovate outline by reduction in the length of the basal pinnae. In addition, a large segment of the *C. protrusa* populations tend toward this outline.

C. APICAL BLADE ATTENUATION. The blade organization typical of the genus in general is a gradual reduction in the size of pinnae toward the apex. This tapering is developed to an extreme in *Cystopteris bulbifera* where the reduction in pinna size progresses over a greater number of pinnae thus resulting in an attenuate blade apex.

D. VENATION PATTERN. In evaluating this character it has been necessary to examine representatives of apparently closely related genera such as *Dryopteris* and *Athyrium* as a guide in determining the primitive condition. In these genera the veins are directed toward marginal teeth. This feature also exists in *Cystopteris protrusa* and *C. fragilis*. The subgenus *Cystopteris* section *Emarginatae*, however, has the veins extending into

emarginations, a distinctive feature among ferns in general. This latter condition is thus considered to be derived.

E. Adaxial epidermal cell walls. Undulating cell walls are correlated with those species of *Cystopteris* which are primitive in several other characters and are thus thought to be the primitive state. Deeply lobed cells are associated with the more specialized taxa.

F. Scales with thickened lateral cell walls. This type of scale is referred to as being "clathrate." It is a characteristic feature of the fern genus *Asplenium*, among others. Within *Cystopteris*, however, it occurs only in *C. sudetica* and its Asian associate *C. pellucida*.

G-H. Indusial cells. Attenuate indusial cells (G) are limited to subgenus *Cystopteris* section *Cystopteris*. The remainder of the genus is characterized by the shorter and more rectangular cells (H).

I. Indusial glands. The glandular indusium is a prominent feature within the genus *Cystopteris* and is construed to be the primitive condition. However, these glands have been lost within each of the evolutionary lines. Both *C. diaphana* and *C. fragilis* show an interesting trend in regard to this character which possibly has some relation to the expansion of their respective ranges. While glandular indusia are universal in the African material of *C. diaphana*, glands are predominantly absent in New World populations. A similar segregation of this character may be observed in *C. fragilis* where the southern element possesses glands while the boreal element apparently lacks these glands completely.

J. Accessory indusial hairs. These multicellular structures are attached to the outer surface of the indusium. They most frequently occur as single hairs but occasionally a more massive aggregation of cells resembling a second indusium is produced. These hairs have been observed solely in *Cystopteris fragilis* and *C. douglasii*.

K. Foliar bulblets. These vegetative reproducing structures occur, within the genus *Cystopteris*, only in *C. bulbifera* and thus their presence is construed to be a specialized feature.

L-M. Multicellular hairs. Non-glandular multicellular hairs (L) are restricted to subgenus *Acystopteris*. The subgenus *Cystopteris* possesses only glandular multicellular hairs (M).

N-P. Spore architecture. The echinate spore (N) is found throughout the subgenus *Cystopteris* while the rugose spore (O) is limited to segments of *C. fragilis*, primarily in the north temperate zone. Spores with highly dissected projections in cross section (P) are confined to the subgenus *Acystopteris*.

An examination of Plate 1 shows that there are two distinct lines of development arising from a prototype which was probably reminiscent of the modern *Cystopteris protrusa*. Subgenus *Acystopteris* resembles the

remainder of the genus in chromosome number and in the position of the indusium. In other respects, such as spore architecture and multicellular hair type, however, this subgenus has become very distinct.

The subgenus *Cystopteris* has evolved along two main lines which are contrasted by such features as vein position, epidermal cells and indusial cells. There are also preliminary indications that these two lines, which are treated as sections of the genus in this work, differ in the marginal profile of the gametophyte.

Within the section *Emarginatae*, the terminal elements of the evolutionary line, namely *C. montana*, *C. sudetica*, *C. pellucida* and *C. bulbifera*, maintain their distinctness throughout their respective ranges and as such are not a problem in the taxonomy of the genus.

Cystopteris diaphana, the fifth member of section *Emarginatae*, presents an entirely different trend for this species apparently mixes extensively with members of section *Cystopteris* (*C. fragilis* and *C. protrusa*). In Plate 1 the shaded area represents the region of apparent interspecific introgression. If a representative collection of *Cystopteris* from North America were plotted on this chart, one would probably find a nearly complete spectrum of variation ranging from the typical plants of *C. fragilis*, *C. protrusa* and *C. diaphana* to various degrees of mixing. The main problem in the "*C. fragilis* complex" then lies in the classification of the intermediate populations.

By critically examining the populations of the "*C. fragilis* complex" from various parts of the North American continent, one can detect certain forms which are relatively distinct in a given region. An example of such a taxon is *Cystopteris fragilis* var. *mackayi* which maintains a distinctive appearance in much of eastern North America. This plant exhibits an intermediate condition between *C. diaphana* and *C. fragilis* in such features as vein position (the veins extending into both marginal teeth and emarginations), epidermal cells and in the shape and organization of the indusium. Other elements, especially from Europe, also have been observed which have a relatively uniform appearance. In the case of such distinctive forms, one might feel obligated to assign a varietal or some other subspecific status. However, when one looks at the whole picture, it becomes almost impossible to define the limits of taxonomic categories where one is dealing not only with these distinct regional elements but also with more subtle differences in varying intensities on a worldwide scale as is demonstrated in Plate 23.

How then can varieties and forms be logically separated when there are various levels and intensities of genetic mixture as well as the more distinctive elements? This is the problem which has been encountered in the study of the "*C. fragilis* complex" and this is the phenomenon which

has apparently led to much of the very extensive nomenclature placed in synonymy in this work. The only apparent way to handle this situation is to regard the three taxa (*C. fragilis*, *C. protrusa*, and *C. diaphana*) as part of a complex including intermediate populations in which only the three extremes are designated as distinct species. The intermediates then, no matter what the degree of similarity to any one of the extremes may be, are then assigned to the complex either as *C. diaphana* × *fragilis* or as *C. diaphana* × *protrusa* depending on the expression of characters.

Taking into consideration the preceding discussion, some authorities may be critical of the stand taken here, namely to maintain a species status for the three extremes of the "*C. fragilis* complex." It might be more prudent to treat these three species as being merely extremes of one widely fluctuating species. Perhaps, because of the worldwide variation pattern and the great extent of intergradation, a better classification would be to consider the extremes as geographical subspecies. This treatment, however, would still not solve the problem relating to the handling of the intermediate populations.

I do not favor this approach in the particular situation at hand even though it would be the logical solution perhaps in other comparable groups of organisms. We are apparently dealing here with a complex in which the extremes, if considered separately, would logically be given specific recognition in any comparable group of plants. *Cystopteris diaphana*, for example, has a great deal more in common with section *Emarginatae* than section *Cystopteris* with respect to its anatomical characteristics. The problem then narrows down to the probability that *C. diaphana* has a genome composition which is very similar to that found in the section *Cystopteris*. A possible explanation for this apparently close genetic similarity may be the maintenance of an ancient gene pool within these species groups whereas the rest of the genus has undergone more extensive genetic modification.

No matter what nomenclatural rank may be assigned to the extremes in the "*C. fragilis* complex" by a given taxonomist, it is quite evident that we are dealing here with a group of plants that have a close genetic relationship. Thus the present study is an excellent example of the problem of assigning categories to a complex taxonomic situation.

TAXONOMIC REVISION

This study includes a detailed treatment recognizing ten species, five varieties and six hybrids or intergrades within the genus *Cystopteris*. Several species for which authentic material has not been obtainable have

been omitted or temporarily referred to other taxa on the basis of the original description.

Furthermore two subgenera are recognized within the genus *Cystopteris*. This division is made necessary because of the inclusion of two Asian species which have some common features with the genus but are totally different in other characters. Also for the first time within the genus *Cystopteris*, sectional categories have been introduced to bring out apparent relationships within the genus. These subdivisions have been especially valuable in the rearrangement of elements which in the past have been relegated to the "catchall" species, *C. fragilis*.

The diagnostic key has been constructed to make use of as many macroscopic characters as possible. However, in some cases a dissecting microscope or even a compound microscope must be utilized to identify a specimen accurately.

Cystopteris

Cystopteris Bernhardi, Schrad. Neu. Journ. 1(2): 26. 1806. (nom. cons.). Internat. Bot. Congress, Cambridge (1930).

Filicula Seguier, Pl. Veron. Suppl. 55. 1754.
Filix Adanson, Fam. d. Pl. 2: 20. 1763.
Cystea Smith Engl. Fl. 4: 260, 284. 1828.
Cyste Dulac, Fl. Haute-Pyrenees 33. 1867.

Small to medium sized ferns primarily of rocky and other epipetric situations but a few species entirely terrestrial, the leaves occurring separately or appearing tufted on rhizome. *Rhizome* compact to wide-creeping, invested with ovate to lanceolate scales. *Stipe* shorter to longer than the blade, stramineous to dark pigmented. *Blade* deltoid or deltoid-attenuate to ovate-lanceolate, bi- to quadripinnatifid; 5-50 cm. long and 2-25 cm. wide; primary pinnae deltoid-lanceolate to ovate-lanceolate, 4-50 pairs, the basal pairs shortly petiolulate, the upper pairs becoming gradually smaller and less dissected; pinnules anadromic. *Lamina* herbaceous to somewhat coriaceous; segment margins lined by jagged cells, ultimate lobes with projecting teeth or depressed emarginations; veins free, entering either teeth or emarginations. *Sorus* dorsal on vein, discrete to sometimes appearing confluent at maturity; indusium attached under the receptacle toward the costa, its free apex arching over the sorus toward the margin of the pinna, ovate-lanceolate to broadly cup-shaped at maturity; sporangia with well developed stalks (except in typical *C. diaphana*), annulus of 13-16 thickened cells (occasionally up to 21); spores bilateral, yellow to dark-brown, echinate or rugose or with short and ridged warts, 27-53 μ long. Basic chromosome number $x = 42$.

Distribution. Worldwide except Antarctica.

Type species. *Cystopteris fragilis* (L.) Bernh.

Diagnostic Key to the Subgenera, Sections and Species of Cystopteris

1. Blade lacking multicellular non-glandular hairs; multicellular glandular hairs present in varying degree; spores echinate or rugose, dark brown ..... Subgenus *Cystopteris.*
2. Veins directed into teeth ..... Section *Cystopteris.*
3. Indusium attached around one-third the circumference of the receptacle
4. Rhizome short creeping with approximate nodes; indusium large and conspicuous; average spore size 32-53 μ ..... 1. *C. fragilis* (introgresses with *diaphana*; hybridizes with *bulbifera* and *montana*)
4. Rhizome wide creeping with distinct internodes; indusium delicate and occasionally fugacious; average spore size 27-32 μ ..... 2. *C. protrusa* (introgresses with *diaphana*)
3. Indusium attached around one-half the circumference of the receptacle ..... 3. *C. douglasii*
2. Veins directed into emarginations ..... Section *Emarginatae*
5. Leaf deltoid, or deltoid-attenuate with lowest pinnae the longest; rhizome cord-like with long internodes
6. Basal pinna with the lowest inferior pinnule longer than the superior pinnule ..... 4. *C. montana*
6. Basal pinna with the lowest inferior pinnule the same length as or shorter than the superior pinnule
7. Scales of stipe and rhizome clathrate; foliar bulblets absent on blade axes; blade approximately deltoid
8. Indusium attached one-half or more of the distance around the receptacle ..... 5. *C. pellucida*
8. Indusium attached about one-third of the distance around the receptacle ..... 6. *C. sudetica*
7. Scales of stipe and rhizome not clathrate; bulblets present on blade axes; blade apically attenuate ..... 7. *C. bulbifera* (hybridizes with *protrusa* and *fragilis*)
5. Leaf ovate-lanceolate with basal pinnae equal to or shorter than the next pinnae; rhizome more robust, with shortened internodes ..... 8. *C. diaphana* (introgresses with *fragilis* and *protrusa*)

1. Blade invested with large multicellular non-glandular hairs; multicellular glandular hairs absent; spores with ridged warts, yellow. Subgenus *Acystopteris*
9. Stipe and rachis with a shiny ebony pigment; unicellular glands absent on lamina and indusium ..... 9. *C. japonica*
9. Stipe and rachis stramineous or light brown; unicellular glands present on lamina and indusium ..... 10. *C. tennisecta*

Subgenus Cystopteris

Small to medium ferns, with deltoid to lanceolate blades; scales of rhizome and stipe glandular or glabrous; stipes shorter to longer than blade; upper stipe, rachis and minor axes with multicellular glandular

hairs; blade bi- to quadripinnatifid; indusium generally cup-shaped at maturity; spores bilateral, dark brown, with echinate or rugose architecture.

Type species. *Cystopteris fragilis* (L.) Bernh.

Two sections are recognized within subgenus *Cystopteris*, namely section *Cystopteris* and section *Emarginatae*.

A. Section Cystopteris.

Veins extending into teeth at the pinna margin; indusium ovate to linear, the free margin frequently lacerate, indusial cells long and narrow (except *C. protrusa* in which the cells approach a rectangular outline); adaxial epidermal cells with deep, irregular lobes.

Type species. *Cystopteris fragilis* (L.) Bernh.

This section contains three species: *Cystopteris fragilis, C. protrusa* and *C. douglasii.*

1a. *Cystopteris fragilis* (L.) Bernh. var. *fragilis*

Polypodium "F. fragile" (a misprint) L. Sp. Pl. 1091. 1753.
Polypodium fragile L. Fl. Suecica, ed. 2. 374. 1755.
Polypodium fragile var. *angustatum* Hoffm. Roem. et Uster. Mag. IX, Pt. 33. Pl. 1. 1790.
Filix fragilis (L.) Gilib. Exerc. Phyt. 558. 1792.
Cyathea fragilis (L.) J. Sm. Mem. Acad. Turin, 5: 417. 1793.
Polypodium dentatum Dickson, Fasc. Pl. Crypt. Brit. 3: no. 1. pl. 7. 1793.
Polypodium anthriscifolium Hoffm. Deutschl. Flora 2: 9. 1795.
Polypodium cynapifolium Hoffm. *ibid.*
Cyathea anthriscifolia (Hoffm.) Roth, Tent. Fl. Germ. 3: 98. 1800.
Cyathea cynapifolia (Hoffm.) Roth, *ibid.*
Aspidium fragile (L.) Sw. Journ. Bot. Schrad. 1800 (2): 40. 1801.
Athyrium fragile (L.) Spreng. Anleit. 3: 136. 1804.
Cystopteris fragilis (L.) Bernh. Neu. Journ. Bot. Schrad. 1(2): 26. pl. 2. f. 9. 1806.
Aspidium dentatum (Dick.) Sw. Syn. Fil. 59. 1806.
Cyclopteris fragilis (L.) Gray, Nat. Arr. Br. Pl. 2: 9. 1821.
Athyrium dentatum (Dick.) Gray, *ibid.* 11.
Cystopteris dentata (Dick.) Desvaux, Prod. Fam. Foug. 6: 263. 1827.
Cystopteris orientalis Desvaux, *ibid.* 264.
Cystea fragilis (L.) Sm. Eng. Fl. 4: 289. 1828.
Cystea dentata (Dick.) Sm. *ibid.* 287.
Cystea angustata Sm. *ibid.* 288.
Cystopteris fragilis var. *angustata* (Hoffm.) Link, Fil. Sp. 46. 1841.
Cystopteris fragilis b. *pinnatipartita* Koch, Syn. Fl. Germ. and Helv. Ed 2. 980. 1845.
Cystopteris fragilis b. *pinnatipartita* 1. *anthriscifolia* (Hoffm.) Koch, *ibid.*
Cystopteris fragilis b. *pinnatipartita* 2. *cynapifolia* (Hoffm.) Koch, *ibid.*
Cystopteris fragilis b. *pinnatipartita* 3. *angustata* (Sm.) Koch, *ibid.*
Cystopteris fragilis var. *vulgaris* Hooker, Sp. Fil. 1: 197. 1846.
Cystopteris fragilis var. *dentata* (Dick.) Hooker, *ibid.* 198.
Cystopteris dickieana Sim, Gardeners' Journ. 308. 1848.
Cystopteris fragilis var. *genuina* Bernoulli, Gefässpfl. der Schweiz. 42. 1857.
Cystopteris fragilis var. *acutidentata* Döll, Fl. Baden 1: 43. 1857.

Cystopteris fragilis var. *rupestris* Neilr. Fl. N. Oest. 13. 1857.
Cystopteris fragilis A. *fragilis* var. *lobulato-dentata* Milde, Sporenpfl. 68. 1865.
Cystopteris fragilis A. *fragilis* var. *pinnapartita* a. *anthriscifolia* (Hoffm.) Milde, *ibid.*
Cystopteris fragilis A. *fragilis* var. *pinnapartita* b. *cynapifolia* (Hoffm.) Milde, *ibid.*
Cystopteris fragilis A. *fragilis* var. *pinnapartita* c. *angustata* (Sm.) Milde, *ibid.*
Cyste fragilis Dulac. Fl. Hautes-Pyrenees. 33. 1867.
Cystopteris baenitzii Dorfler in Baenitz, Herb. Eur. n. 6510. 1891.
Cystopteris fragilis subsp. *eu-fragilis* var. *Baenitzii* (Dorfl.) Warnst. in Aschers. Graebn. Syn. Mit. Eur. Fl. 1: 17. 1896.
Cystopteris fragilis var. *anthriscifolia* subvar. *favrati* Christ, Farnk. Schw. 156. 1900.
Cystopteris fragilis var. *dentata* subvar. *tavelii* Christ, *ibid.* 158.
Cystopteris fragilis var. *dentata* subvar. *woodsioides* Christ, *ibid.*
Cystopteris polymorpha Bubani, Fl. Pyr. 4: 431. 1901.
Cystopteris fragilis var. *dickieana* (Sim) Lindberg., Medd. Soc. Fauna et Flora Fennica. 32: 21-24. 1905.
Cystopteris fragilis subsp. *dickieana* (Sim) Hylander, Uppsala Univ. Arsskr. 1945 (7): 59. 1945.

Rhizome short creeping, internodes very short, leaves and old stipe bases approximate, clustered near rhizome apex; scales lanceolate, reddish-brown, abundant near apex, glabrous. *Stipe* shorter than blade, stramineous to lustrous dark brown, with lanceolate scales at base. *Blade* bipinnate to tripinnatifid, ovate-lanceolate, up to 30 cm. long and 12 cm. wide; rachis and minor axes with scattered uni- and multicellular glandular hairs; primary pinnae ovate to ovate-lanceolate, subopposite to alternate, from 1-8 cm. long and 0.5-4.0 cm. wide; basal secondary pinnae shortly petiolulate, the remainder adnate, ovate to lanceolate, with obtuse to acute apices, apices of lobes terminated by rounded or acute teeth into which veins are directed. *Sori* round, discrete to overlapping at maturity; indusium ovate to lanceolate, mostly with lacerate apex, glabrous, cells long attenuate with conspicuous accessory indusial hairs; sporangium with well-developed stalk; spores echinate, dark brown, size 32-53 μ. Chromosome numbers, n = 84, 126, 168. (Plate 2)

Distribution. Panboreal, into Mexico, eastern Africa, Ceylon.

Type. Not seen. Copeland (1929) states that the type specimen is in the herbarium of the Linnean Society, London. However, Stearn of the British Museum states (personal communication with R. L. Hauke, 1957) that none of the current specimens of *C. fragilis* in the Linnaean Herbarium were available when the original description was written.

Linnaeus did refer to an illustration in Plukenet's *Phytographic*, however, and Stearn further stated that the type of this illustration is H. S. (Herb. Sloan) 96, Folio 40. If no other type has been designated, this would be the logical specimen to choose.

Discussion. The specific epithet "F. fragile" is quite obviously an error as was pointed out by Weatherby (1926) in his discussion of the problem. This same error has obviously resulted in the formation of the binomial *Filix fragilis.*

Cystopteris dentata is merely a variation of *C. fragilis* in which the ultimate lobes are rounded and the marginal teeth are not acute. Link's

description of *C. rhaetica* places this species as a form of limited distribution in central Europe.

The plants of *Cystopteris dickieana* from the type locality of Aberdeen, Scotland (illustrated by Newman, British Ferns, 1954), are distinctive macroscopically in that the pinnae arise in close proximity to each other so that there is abundant overlapping. These plants apparently retained their macroscopic characteristics in culture (Sowerby, 1859). The only other feature which distinguishes this fern from *C. fragilis* var. *fragilis* is the spore architecture and intermediate conditions have been observed between the rugose spore and echinate spore. As this spore type within *C. fragilis* has a wide geographic range and there are apparent transitional spores, it seems worthy only of designation as a spore form within *C. fragilis*. The imbricate pinnae of the type collection has not been found to be correlated with the spore condition.

A specimen of the type collection of *Cystopteris baenitzii* has been examined and the plants are typical *C. fragilis* var. *fragilis* but with the rugose spores, like those of Dickie's plant.

The abundance of synonyms reflects the diversity of *Cystopteris fragilis* var. *fragilis*. In addition, this species, which is abundant in Europe, has been studied in some detail, resulting in new names and recombinations of old names. Some of the binomials included in my synonymy of this variety may actually represent plants in which introgression with *C. diaphana* has occurred. As authentic specimens have not been available, however, these names have been included under *C. fragilis* var. *fragilis*. Luerssen (1889) attempted a partial synonymy of binomials for this species which seems to be, in the main, accurate. I have, however, removed some names which do not belong there according to my interpretation of var. *fragilis*.

1b. *Cystopteris fragilis* var. *apiiformis* (Gandoger) C. Chr.

Cystopteris apiiformis Gandoger, Bull. Soc. France *60:* 28. 1913.
Cystopteris apiiformis = *C. fragilis* var., C. Chr. Ind. Fil. Suppl. 1913-1916.

Similar to *Cystopteris fragilis* var. *fragilis* but indusium glandular; and veins mostly not extending to margin. (Plate 19)

Distribution. New Zealand, southern South America and adjacent islands, Kerguelen Island.

Type. "Ins. Falkland, prope West F. Roy Cove. Skottsberg n. 61." An isotype is in S-PA.

Discussion. Christensen quite obviously intended to make the varietal combination although he worded it as found in the synonymy. *Cystopteris novae-zealandiae* Armstrong and *C. laciniatus* Colenso probably belong here

but as authentic material has not been seen they are not included in the synonymy.

The bulk of the New Zealand specimens have a very characteristic appearance, the bipinnate fronds being much attenuated and the pinnae widely separated, with teeth very shallow. The South American material has broader, more ample fronds which occasionally approach a tripinnatifid condition. The Kerguelen Island population, while still possessing indusial glands, has veins which reach the margins of the pinnae, thus approaching more closely the typical variety.

In these three regions of the southern hemisphere, therefore, *Cystopteris fragilis* is represented by three populations of a variety which have significant features in common. It is postulated that this variety is primitive within the species because of the presence of indusial glands. The vein condition is reminiscent of that found in many species of *Dryopteris* and is universal in the genus *Woodsia* (Brown, 1958).

1c. *Cystopteris fragilis* var. *huteri* Hausman, ex Milde Fil. Eur. 149. 1867.

Similar to *Cystopteris fragilis* var. *fragilis* but with lamina copiously invested with unicellular glands especially on the margins; rachis and frequently the minor axes with long uniseriate multicellular hairs, commonly capped by a dark brown globose gland cell; indusium remaining glabrous. (Plate 19)

Distribution. Limited to the mountainous regions of western and central Europe.

Type. Not seen. "Tirol: Pusterthal. In rup. dolomit. (Huter)." The specimens at hand agree closely with the original description which I have seen.

Discussion. Specimens from the type region of Tirol are very uniform, with a dissected appearance somewhat resembling that of *C.* × *alpina* macroscopically but lacking emarginate teeth. It is a very distinctive segregate of *C. fragilis* with a greatly restricted range.

2. *Cystopteris* protrusa (Weath.) Blasdell comb. nov.

Cystopteris fragilis var. *protrusa* Weath. Rhod. 37: 373. 1935.

Rhizome wide-creeping with distinct internodes, apex protruding 2-4 cm. beyond current season's leaves; scales lanceolate, sparse. *Stipe* shorter than blade, stramineous; scales sparse at base. *Blade* bipinnatifid to bipinnate, deltoid to ovate lanceolate, up to 22 cm. long and 12 cm. wide; minor axes with scattered uni- and multicellular glands; primary pinnae subopposite to alternate, petiolulate, ovate to ovate-lanceolate; secondary pinnae at base of blade frequently short petiolulate, pinnatifid into oblong, obtuse lobes; veins typically running into marginal teeth. *Sori* round, discrete to occasionally overlapping at maturity; indusium minute, delicate, occasionally apparently fugacious, ovate, entire at apex, glabrous, with somewhat elongate cells, accessory indusial hairs not observed; spores echinate, dark brown, size 27-32 μ. Chromosome number n = 42. (Plate 3)

Distribution. New York to Georgia, westward to Wisconsin and Arkansas.

Type. Tennessee, Knoxville, June 5, 1898. Ruth 564 (GH!).

Discussion. Cystopteris protrusa is a very distinct species of eastern United States and has features which are considered primitive within the genus. It possesses a creeping rhizome with the apex protruding far beyond the current growth. This species is also the only known member of section *Cystopteris* which possesses the diploid chromosome number.

While *Cystopteris protrusa* occurs in its typical form (deltoid blades) primarily in the Appalachian Mountain system, its form in populations to the west becomes very similar to that of *C. fragilis* var. *fragilis*. All the characters except blade pattern, however, resemble those of *C. protrusa*.

Cystopteris protrusa is considered to be a parent of the putative hybrid *C.* × *tennesseensis*. There is also some evidence of apparent introgression between *C. protrusa* and *C. diaphana* which is indicated most frequently by the presence of both types of vein termination.

3. *Cystopteris douglasii* Hooker, Sp. Fil. 1: 200. 1846.

Cystopteris sandwicensis Brack., Expl. Exp. 16: 234. 1854.

Rhizome short creeping, internodes short, resulting in clumping of leaves near apex, sparsely invested with brown lanceolate scales. *Stipe* shorter than blade, stramineous to light brown, scales lanceolate, only at base of stipe. *Blade* bipinnatifid to bipinnate, deltoid to ovate-lanceolate, up to 25 cm. long and 12 cm. wide; rachis and minor axes sparsely invested with uni- and multicellular glandular hairs; primary pinnae shortly petiolulate, subopposite to alternate, broad-ovate; secondary segments not petioled, ovate, with dentate serrations some of which are emarginate, some of veins may enter emarginations. *Sori* round, discrete to overlapping at maturity; indusium cup-shaped, broadly attached under receptacle, glabrous, indusial cells somewhat elongate, invested with accessory indusial hairs; spores dark brown, echinate, size 43-53 μ. Chromosome number n = ca. 168. (Plate 4)

Distribution. Hawaiian Islands.

Type. Not seen. It is "Sandwich Islands, D. Douglas, n. 51" and is probably at K.

Discussion. Cystopteris douglasii is close to *C. fragilis* and is endemic to the Hawaiian Islands. Superficially it resembles *C. bulbifera* with its twice pinnate lanceolate fronds but it is not as highly dissected. The indusium of *C. douglasii* is rather broadly attached and its cells are somewhat shorter than those in *C. fragilis*. However, the accessory indusial hairs are common to both species.

While typical *C. douglasii* has an ovate-lanceolate blade there is a form with rather wide, sub-deltoid blades which has been described as *C. sandwicensis*. Except for a slight increase in dissection, however, the type specimen (Kaala Mt., Wainai, Sandwich Islands, Wilkes Exped. 1838-42) shows no obvious difference from *C. douglasii*. They are accord-

ingly being maintained as one species. Since the above work was carried out, further spore observations in this species indicate that there may be another polyploid level represented in the range of 4n or 6n.

B. Section Emarginatae

Section *Emarginatae* Blasdell sectio novum.

Cystopteris with veins extending into depressions at the pinna margin; indusium cup- or fingernail-shaped, the free margin relatively entire, indusial cells roughly rectangular in outline; adaxial epidermal cells with regular walls or merely shallow, regular lobes.

Type species. *Cystopteris montana* (Lam.) Bernh.

Sectio *Emarginatae* Blasdell sectio novum.

Cystopteris venulis in depressiones prope marginem pinnae excurrentibus; indusio calyciformi aut unguiformi, margine libero plus magis integro, cellulis indusii circumscriptione fere rectangulari; cellulis adaxialibus epidermalibus circumscriptione regulari aut lobis tantum haud profundis, regularibus. Species typica; *Cystopteris montana* (Lam.) Bernh.

Section *Emarginatae* is set up to delimit a segment of subgenus *Cystopteris* with the following characters in common: vein position, indusial structure and adaxial epidermal cell outline. This section consists of five species: *Cystopteris montana, C. pellucida, C. sudetica, C. bulbifera* and *C. diaphana.*

4. *Cystopteris montana* (Lam.) Bernh. Neu. Journ. Bot. Schrad. 1(2):26. 1806.

Polypodium montanum Lam. Fl. Franc. 1: 23. 1788.
Cyathea montana (Lam.) J. Sm. Mém. Acad. Turin 5: 417. 1793.
Aspidium montanum (Lam.) Sw. Journ. Bot. Schrad. 1800 (2): 42. 1801.
Athyrium montanum (Lam.) Rohl. ex Spreng. Anleit. 3: 143. 1804.
Cystopteris allioni Newman, The Phytologist 1851. app. XXV.
Cystopteris myrrhidifolia Newman, Hist. of Brit. Ferns Ed. III. 97. 1854.
Cyste montana (Lam.) Dulac, Fl. Hautes-Pyrenees 33. 1867.
Polypodium myrrhidifolium Vill. ex Gilibert, Syst. Plant. Eur. I: 114. 1875.
Filix montana (Lam.) Underw. Our Nat. Ferns, Ed. VI, 119. 1900.
Filicula montana (Lam.) Farwell, Am. Mid. Nat. 12: 252. 1931.

Rhizome cord-like, up to 3 mm. in diameter, wide-creeping, internodes extensive, up to 4.0 cm. long, with leaves borne separately, apex invested with large light brown ovate-lanceolate scales. *Stipe* characteristically longer than the blade, occasionally up to 3 times as long, stramineous, invested with large light brown ovate-lanceolate scales up to 6 mm. long and 3 mm. wide with glandular margin. *Blade* quadripinnatifid, broadly deltoid, up to 15 cm. long and 19 cm. wide, the two basal pinnae longer than blade length but frequently arched toward blade apex resulting in a more equilateral deltoid blade; primary pinnae subopposite to alternate, short-petiolulate, the lowest pair longest and the upper pinnae becoming successively smaller, the basal pinnae unsymmetrically triangular resulting from the lengthening of the inferior costal pinnule; tertiary segments pinnatifid with emarginations into which the ultimate veins are directed. *Sori* round, discrete to overlapping at maturity; indusium shallowly cup-

shaped, cells roughly rectangular, invested with primarily marginal unicellular glands; spores dark brown, echinate, size 27-42 μ. Chromosome number n = 42, 84. (Plate 5)

Distribution. China, northern India, USSR, Europe, Canada and the United States.

Type. Not seen. The original description which I have examined agrees with the available specimens of this species.

Discussion. The similarities between *Cystopteris montana* and *C. sudetica* are rather imposing. The features which are characteristic of *C. montana*, however, are the greater size of the inferior rachal pinnules as compared with the superior pinnules of the basal pinnae. *Cystopteris montana* also lacks the clathrate scales which are characteristic of *C. sudetica*. There are also fewer glands on the indusia of *C. montana* than in *C. sudetica* and they are limited primarily to the margins.

It is suggested that *Cystopteris montana* has been involved in the production of two described hybrids, namely *C. fragilis* × *montana and C.* × *alpina*. The evidence for these views is strictly morphological and anatomical.

5. *Cystopteris pellucida* (Franch.) Ching ex C. Chr. Ind. Supply. III. 67. 1934.

Aspidium pellucidum Franch. Nouv. Arch. Mus. II 10: 119. 1887.
Dryopteris pellucida (Franch.) C. Chr. Ind. 283. 1905.

Rhizome creeping, internodes extensive, scales clathrate, brown, eglandular, sparse. *Stipe* up to 2 times as long as blade, light green to stramineous, with clathrate scales at base. *Blade* tripinnatifid to tripinnate, deltoid to deltoid-lanceolate, up to 25 cm. long and 13 cm. wide, the lower pinnae frequently directed toward blade apex; basal pinnae short-petiolulate, ovate lanceolate, up to 9 cm. long and 4 cm. wide; secondary pinnae pinnatifid to pinnate, ovate, with emarginations into which the ultimate veins are directed. *Sori* round, discrete to slightly overlapping at maturity; indusium cup-shaped, attached up to 2/3 of the circumference of the receptacle, cells roughly rectangular, glabrous; spores echinate, dark brown, size 27-32 μ. Chromosome number n = 42. (Plate 6)

Distribution. Yunnan and Moupin provinces, China.

Type. Not seen. "Moupine, in silvis humidis umbrosis, *David*, Aug 1869." It is probably located in P. The original description has been studied and agrees closely with the specimens at hand.

Discussion. As one of several Asian species which appear to be closely related to *Cystopteris sudetica* this fern has a rather restricted distribution. It resembles *C. sudetica* var. *sudetica* in blade outline and in the possession of clathrate scales. It differs in the eglandular indusium and in the broad attachment of the indusium to the receptacle. Another feature is the reduction in dissection of this plant as compared with that in *C. sudetica*. A specimen collected by David in 1870 has blades which, while still broadest at the base, have a more lanceolate outline than the other specimens seen.

6a. *Cystopteris sudetica* var. *sudetica*

Cystopteris sudetica A. Br. et Milde, Jahresber. scheles. Ges. 1855: 92.
Cystopteris leucosoria Schur, Oest. Bot. Zeit. 8: 328. 1858.
Cystopteris leucospora Schur, *ibid.*
Cystopteris sudetica var. *vulgaris* Milde, Sporenpfl. 71. 1865.
Cystopteris sudetica var. *leptophylla* Milde, *ibid.*
Cystopteris sudetica var. *platyphylla* Milde, *ibid.*
Cystopteris braunii Milde, in lit. ex Milde, *ibid.*
Cystopteris silesiaca A. Br. in lit. ex Milde, *ibid.*

Rhizome slender, up to 2 mm. in diameter, wide-creeping, internodes up to 4 cm. long with leaves occurring singly; scales clathrate, most conspicuous near apex. *Stipe* longer than blade, being frequently 2 to 3 times as long, stramineous; clathrate scales up to 3 mm. long and 2 mm. wide, with glandular margins, scattered toward base of stipe. *Blade* tripinnate to quadripinnatifid, broadly deltoid, up to 19 cm. long and 20 cm. wide (the 2 basal pinnae longer than blade length but generally curved toward blade apex); rachis and minor axes with occasional unicellular and multicellular glandular hairs; primary pinnae predominantly alternate, short petiolulate, the lowest pair longest, the upper pinnae being successively smaller, terminating in a pinnatifid apex, ovate lanceolate; secondary pinnae ovate, inferior pinnule of basal pinna the same size as superior pinnule, secondary pinnae approximate and frequently overlapping; tertiary segments of lower pinnae pinnatifid or merely toothed, with apices of teeth emarginate; vein endings directed into emarginations. *Sori* round, discrete or rarely overlapping when mature, dorsal on vein; indusium cup-shaped, cells roughly rectangular, invested with unicellular glands; spores with echinate architecture, dark brown, 27-32 μ. Chromosome number n = 42. (Plate 7)

Distribution. Norway and western Russia but primarily concentrated in the mountainous regions of central Europe.

Type. Not seen. The original description has been examined and agrees with the available specimens from central Europe.

Discussion. The superficial morphology of *Cystopteris sudetica* resembles very closely that found in *C. montana* and, indeed, these two species appear to be closely related. They have in common the long cord-like rhizome with extended internodes. They also have the same deltoid blade plan and similar features of the indusium. They differ, however, in two respects. *Cystopteris sudetica* lacks the extended inferior costal pinnule which is so characteristic of the basal pinnae of *C. montana*. Also *C. sudetica* var. *sudetica* has the distinctive clathrate scales which also occur in its Asian relatives. From *C. sudetica* var. *moupinensis* it differs in its greater dissection and in the presence of indusial glands.

6b. *Cystopteris sudetica* var. *moupinensis* (Franch.) Blasdell comb. nov.

Cystopteris moupinensis Franch. Nouv. Arch. Mus. II 10: 111. 1887.
Cystopteris sphaerocarpa Hayata, Ic. Pl. Form. 4: 144. f. 84. 1914.
Cystopteris modesta Ching, Bull. Fan Mem. Inst. Biol. 10: 5-6. 1940.

Differing from *Cystopteris sudetica* var. *sudetica* in less dissection (tripinnatifid to tripinnate) of the blade and in the lack of glands on the indusium. (Plate 19)

Distribution. Region of Moupine, Yunnan, Sikang, Kansu, Shensi and Szechuan provinces, China.

Type. Not seen. "Moupine, in rupibus adumbratis" David, Aug. 1869. This specimen is probably in P.

Discussion. The placement of *Cystopteris sphaerocarpa* here is based partially on a photograph of the type specimen indicating a close identity to *C. sudetica* var. *moupinensis.* Hayata, in his discussion, refers only to a slight difference in dissection in contrasting the two taxa.

Cystopteris modesta differs from *C. sudetica* var. *moupinensis* in increased dissection and larger indusia. Also noted in Ching's discussion is the fact that "the apices of the segments are always reflexed, covering part of the sori in the manner of *Hypolepis.*" He further comments that this condition may be due to the dryness of the season. It seems best to refer *Cystopteris modesta* to the present variety unless authentic material can be examined and the differences be shown to be more substantial than those described.

7. *Cystopteris bulbifera* (L.) Bernh. Schrad. Neu. Journ. 1 (2) : 10. 1806.

Polypodium bulbiferum L. Sp. Pl. 2: 1091. 1753.
Aspidium bulbiferum (L.) Sw. Schrad Journ. 1800 (2): 41. 1801.
Nephrodium bulbiferum (L.) Michx. Fl. bor. Am. 2: 268. 1803.
Aspidium atomarium Muhl. ex Willd. Sp. Pl. 5: 279. 1810.
Athyrium atomarium (Muhl.) Pr. Rel. Haenk. 1: 40. 1825.
Cystopteris atomaria (Muhl.) Pr. Tent. 93. 1836.
Cystopteris bulbifera var. *flagelliformis* Lawson, Edinb. New Philos. Journ. 19: 280. 1864.
Cystopteris bulbifera var. *horizontalis* Lawson, *ibid.*
Cystea bulbifera (L.) Watt, Can. Nat. II. 13: 160. 1867.
Filix bulbiferum (L.) Und. Our Nat. Ferns Ed. VI. 119. 1900.
Cystopteris bulbifera forma *horizontalis* (Lawson) Gilbert, List N. Am. Pterid. 16. 1901.
Filicula bulbifera (L.) Farwell, Am. Mid. Nat. 12: 251. 1931.
Filicula bulbifera var. *horizontalis* (Lawson) Farwell, *ibid.*

Rhizome creeping, with short internodes, heavily invested with old stipe bases, scales lanceolate, abundant at apex of rhizome. *Stipe* much shorter than blade length, pink to stramineous, scales limited to base. *Blade* bipinnate to tripinnatifid, attenuate-deltoid, up to 5 ft. long and 5 in. wide at base; rachis and minor axes producing scattered fleshy vegetative propagules (bulblets) and invested with uni- and multicellular glandular hairs; primary pinnae subopposite to alternate, up to 30 pairs, short-petiolulate, ovate-lanceolate to oblong, up to 7.5 cm. long and 5.0 cm. wide; secondary pinnae sessile, pinnatifid, with small rounded emarginate teeth, ultimate veins directed into emarginations. *Sori* round, discrete; indusium cup-shaped, broadly attached under the receptacle, cells short rectangular, typically invested with unicellular glandular hairs; spores dark brown, echinate, size 27-32 μ. Chromosome number n = 42. (Plate 8)

Distribution. Newfoundland to Manitoba, south to Georgia and central Arizona, Guadelupe Mts., New Mexico.

Type. Not seen. As is the case with *Cystopteris fragilis*, a type was not cited in the original description. However, as reference is given to Plu-

kenet's Phytographie, this illustration would be the logical type of the species.

Discussion. This is a very distinct species primarily of central and eastern United States and Canada. Its attenuate tapering frond, broadly attached indusia and the occurrence of vegetative propagules on the axes are the prime diagnostic features. The bulblets are most frequently glabrous except for a few multicellular glandular hairs. However, occasionally specimens are found in which the bulblets are provided with light brown scales. The indusia, while typically glandular, are occasionally glabrous.

Cystopteris bulbifera is evidently a parent of the putative hybrids, *C.* × *tennesseensis* and *C.* × *laurentiana*. Since *C. bulbifera* occurs throughout the ranges of these hybrids, the respective ranges of these intermediates are determined primarily by the distribution of the other parents, diploid *C. protrusa* versus the tetraploid *C. fragilis*.

8. *Cystopteris* **diaphana** (Bory) Blasdell comb. nov.

Polypodium diaphanum Bory, Voyage Iles Mers Afr. I. 328. 1804.
Athyrium fumarioides Presl, Rel. Haenk. I. 39. 1811.
Cystopteris canariensis Presl, Tent. Pterid. 93. 1836.
Cystopteris fragilis var. *nigrescens* Hook. Sp. Fil. 1: 198. 1846.
Cystopteris azorica Fee, Gen. Fil. 300. 1850-52.
Cystopteris fragilis var. *azorica* (Fée) Moore, Ind. Fil. 282, 1857-62.
Cystopteris fragilis var. *sempervirens* Moore, *ibid.*
Cystopteris fragilis subsp. *alpina* var. *canariensis* (Presl) Milde, Fil. Eur. 152. 1867.
Cystopteris fragilis subsp. *regia* var. *canariensis* (Presl) Aschers. Synop. Mit. Eur. Fl. 1: 18. 1896.
Cystopteris fragilis subsp. *canariensis* (Presl) Christ, Farnkr. Schweiz. 158. 1900.
Asplenium diaphanum Lojacono, Fl. Sic. 3: 402, tab. VI, fig. 4. 1909.
Cystopteris fragilis subsp. *diaphana* (Bory) Litard., Bull. Soc. Bot. Deux-Sevres, 88. 1911-12.

Rhizome short creeping, internodes short, leaves somewhat clumped near apex, only sparsely invested with dark brown lanceolate scales except at apex, scales occasionally with marginal glands. *Stipe* shorter than the blade, stramineous to medium brown, with some scales at base. *Blade* bipinnate to tripinnate, ovate-lanceolate, up to 30 cm. long and 14 cm. broad; rachis and minor axes with scattered uni- and multicellular glandular hairs; primary pinnae subopposite to alternate, basal pinnae short petiolulate, ovate-lanceolate, obtuse; secondary pinnae obtuse, with emarginations, veins running into emarginations. *Sorus* round, discrete to running together when mature; indusium fingernail- to cup-shaped, with entire rounded apex, cells roughly rectangular, glandular to glabrous; sporangia with much shortened stalks; spores dark brown, echinate, spore size 27-48 μ. Chromosome number n = 42, 84, 126. (Plate 9)

Distribution. Canary Islands, Tanganyika Territory, Mexico, South America.

Type. Not seen. The original description was formulated from plants collected on Reunion Island and agrees with both the African and the South American specimens I have seen.

Discussion. This species, in the past, has been combined with *Cystopteris fragilis* and has been designated by various infraspecific categories. The most recent treatment has been that by Litardière (1912) in which *C. diaphana* was given a subspecific status based primarily on the vein condition and the glandular indusia. He also outlined the distribution of this element which is dominantly southern.

The resemblance of *Cystopteris fragilis* to *C. diaphana* is superficially very great since they both have the ovate-lanceolate type of blade. *Cystopteris diaphana,* however, has certain anatomical features which are quite distinct. Besides the vein characters, *C. diaphana* has adaxial epidermal cells which have straight or merely undulating walls and are somewhat rectangular as opposed to the deeply lobed cells of *C. fragilis.* Also the indusial cells are rather short and rectangular as contrasted with the attenuate cells of *C. fragilis.* Finally, the sporangial stalk of *C. diaphana* is very much reduced (except in certain introgressant populations) so that the sporangium appears essentially sessile. Careful dissections, however, show the stalk cells which are much shortened. The remainder of the species in the genus possess well developed sporangial stalks.

While these characters remain quite distinct where *Cystopteris diaphana* is isolated from *C. fragilis,* they do not correlate well where the ranges of these two species overlap. Apparently large scale gene exchange occurs where these species occur sympatrically.

Subgenus Acystopteris

Subgenus *Acystopteris* (Nakai) Blasdell stat. nov.

Acystopteris Nakai, Bot. Mag. Tokyo. 47: 180. 1933. (pro gen.).

Medium sized ferns with deltoid blades; scales with glandular margins on the stipe base and rhizome apex; stipes nearly equalling length of blade, invested with colorless multicellular non-glandular hairs; blade at least tripinnatifid; indusium merely a small flap subtending sorus (not cup-shaped); spores bilateral, yellow, warts of exospore much dissected in cross section.

Type species. Cystopteris japonica Luerssen.

Subgenus *Acystopteris* includes two species: *Cystopteris japonica* and *C. tenuisecta.*

9. *Cystopteris japonica* Luerssen, Bot. Jahr. f. Syst. 4: 363. 1883.

Acystopteris japonica Nakai, Bot. Mag. Tokyo 47: 180. 1933.
Cystopteris japonica var. *taiwaniana* Tagawa, Act. Phytotax. Geobot. 4: 51-57. 1935.

Rhizome creeping, up to 6 mm. in diameter, internodes distinct but short, resulting in grouping of leaves near apex; scales ovate-lanceolate with glandular margins, dark brown, predominantly near rhizome apex. *Stipe* and rachis (and sometimes costa bases)

a shiny black color, with lanceolate, brown, glandular-margined scales throughout the stipe; stipe length approaching length of blade. *Blade* tripinnate, deltoid, up to 35 cm. long and 30 cm. wide, lower pinnae frequently curved toward blade apex, rachis and minor axes provided with multicellular non-glandular hairs; primary pinnae subopposite in lower half of blade, bipinnate, subsessile, long lanceolate, upper pinnae lanceolate and simply pinnate; secondary pinnae opposite to alternate, sessile, elongate-lanceolate; veins of ultimate segments pinnately organized with most veins running into marginal teeth. *Sori* round, discrete, single on the anterior vein branch of the ultimate segments (except for basal pinnae) thus forming two rows parallel with costa of secondary pinna, pale brown; indusium round-ovate, completely obscured in the mature sorus, glabrous, cells short rectangular; spores yellowish, thickly invested with short ridged warts, size 28-37 μ. Chromosome number = 42, 84?. (Plate 10)

Distribution. Kweichow and Szechwan provinces, China to Honshu, Japan.

Type. Not seen. "Kiusiu, Osumi, Hezukumura (Tachiro)." It may have been in the herbarium at Leipzig and if so was destroyed in the Second World War. The specimens at hand agree closely with Luerssen's original description of the species.

Discussion. This species and the closely related *Cystopteris tenuisecta* are quite distinct from the remainder of the genus having in common only the position of the sorus and the basic chromosome number. They have the distinctive features of spore architecture, multicellular non-glandular hairs and epidermal cells on a more diminutive size scale.

Cystopteris japonica differs from *C. tenuisecta* in the possession of a glossy black stipe and rachis. This dark pigment may even extend into the axes of the pinnae. Another diagnostic character is the absence of glands on the indusium. The indusium is very minute and would not appear to serve extensively in the protection of the young sorus.

10. *Cystopteris tenuisecta* (Bl.) Mett., Ann. Lugd. Bat. 1: 241. 1864.

Aspidium tenuisectum Bl. Enum. Plant. Javae. Fasc. II. Filices. 130. 1828.
Alsophila tenuisecta Bl. ex Moore Ind. Fil. 58. 1857-62.
Athyrium tenuisectum (Bl.) Moore, *ibid.* 188.
Asplenium (Athyrium) tenuisectum Hooker, Sp. Fil. 3: 222. 1860.
Lastrea setosa Bedd. Ferns Br. Ind. t. 262. 1869.
Cystopteris setosa Bedd. *ibid.* t. 312.
Davallia setosa (Bedd.) Baker Syn. Fil. 468. 1874.
Cystopteris formosana Hayata, Ic. Plant. Form. 143-146. 1914.
Acystopteris tenuisecta Tagawa, Acta Phytotax. Geobot. 7: 73. 1938.

Rhizome creeping, robust, internodes short but distinct, resulting in grouping of leaves near apex; scales ovate-lanceolate, glandular-margined, most prevalent near rhizome apex. *Stipe* glossy, stramineous, with lanceolate, glandular-margined, brown scales scattered throughout, stipe approaching length of blade. *Blade* tripinnate to quadripinnatifid, deltoid, up to 50 cm. long and 25 cm. broad; rachis and minor axes invested with multicellular non-glandular hairs; primary pinnae subopposite in the lower half of the blade and bipinnate, long lanceolate; upper pinnae lanceolate, pinnate, alternate; secondary pinnae opposite to alternate, sessile, elongate-lanceolate; veins of ultimate segments pinnately organized with most veins running into marginal teeth. *Sori* round, discrete, single on the anterior vein of the ultimate segments thus forming 2

rows parallel to the ultimate costae, pale brown; indusium round-ovate, cells short rectangular, invested with unicellular glands; spores yellowish, thickly covered with short ridged warts, size 28-32 μ. Chromosome number n = 42. (Plate 11)

Distribution. Northeast India eastward to Honshu, Japan, southward to Java and the Philippine Islands.

Type. "Crecit in sylvis temperatis insulae Java. Blume." (L!).

Discussion. This species is quite evidently closely related to *Cystopteris japonica*. Its primary distinctive features are the presence of glands on the indusium and in the lack of dark pigment on the primary axes of the leaf.

The description by Beddome of *Lastrea setosa* was based on rather poor material. Later in the same publication he transferred this plant to *Cystopteris* based on more adequate material.

Cystopteris formosana is placed here on the basis of the original description. Hayata states in his discussion of the species that it is perhaps a smaller form of *C. setosa* (now referred to *C. tenuisecta*).

Hybrids

1. *Cystopteris* × *tennesseensis* Shaver (pro spec.).

Cystopteris fragilis f. *simulans* Weatherby, Rhodora 37: 376. 1935.
Cystopteris tennesseensis Shaver, Journ. Tenn. Acad. Sci. 25 (2): 107. 1950.
Cystopteris fragilis var. *tennesseensis* (Shaver) McGregor, Am. Fern Journ. 40: 202. 1950.
Cystopteris fragilis var. *simulans* (Weath.) McGregor, Am. Fern Journ. *ibid.*

Rhizome creeping, internodes short with leaves tufted near apex, apex invested with numerous lanceolate scales. *Stipe* mostly dark brown at base gradually becoming stramineous toward blade, predominantly shorter than blade. *Blade* bi- to tripinnatifid, deltoid to deltoid-lanceolate, up to 31 cm. long and 18 cm. wide; minor axes with scattered uni- and multicellular glandular hairs, bulblets present or absent on rachis; primary pinnae subopposite to alternate, short petiolulate, broadly ovate; secondary pinnae mostly petiolulate toward base of blade but broadly attached above, obtuse, cut into lobes which are also obtuse, with marginal teeth and emarginations; veins directed both into teeth and emarginations. *Sori* round, discrete to occasionally coenosoral; indusium cup-shaped with truncate apex, rather broadly attached under receptacle, cells roughly rectangular, with or without unicellular glands; spores dark brown, echinate, size 32-42 μ. Chromosome number n = 84. (Plate 12)

Distribution. Maryland south to North Carolina, west to Kansas and Oklahoma.

Type. Not seen. "Quarry, Round Lick Creek, near the Cumberland River, Rome, Smith Co., Tennessee. Shaver no. 7885." I have seen numerous collections by Shaver of this plant and they agree closely with specimens throughout the range described above.

Discussion. This putative hybrid appears to combine the characters of *Cystopteris protrusa* and *C. bulbifera*. The features which are diagnostic of *C. bulbifera* are the broad frond base and the frequent occurrence of

bulblets as well as occasional glands on the indusium. It also usually has the acuminate (but not long attenuate) apex of *C. protrusa*. Only rarely does the leaf show a tendency to become attenuate. The putative parents are both diploids, resulting in a tetraploid hybrid which is the case with *C.* × *tennesseensis*. It is interesting to note that *C.* × *tennesseensis* has not been reported outside the range of *C. protrusa*. Shaver (1950) was the first to publish the parentage of this hybrid although a hybrid origin had been suggested by Weatherby (in Wherry, 1944) and Wagner (1944).

Cystopteris fragilis form *simulans* is quite evidently referable to this hybrid. McGregor (1950) acknowledges their close relationship but maintains them as two varieties of *C. fragilis*. They both occupy the same geographic regions and are so similar that it is thought best to unite them. The lack of glands in some specimens may possibly be explained by the fact that some specimens of *C. bulbifera* (the presumed parent which supplies the glands to the hybrid) are eglandular.

2. *Cystopteris* × **laurentiana** (Weath.) Blasdell comb. novum

Cystopteris fragilis var. *laurentiana* Weatherby, Rhodora, 28: 129. 1926.

Rhizome creeping, with short internodes, leaves tufted near apex; scales lanceolate, prominent near apex. *Stipe* shorter than the blade, light brown to red-tinged. *Blade* tripinnatifid, ovate-attenuate, up to 34 cm. long and 13 cm. wide; rachis occasionally with bulblets, minor axes with scattered uni- and multicellular glandular hairs; primary pinnae subopposite to alternate, short petiolulate, broadly ovate; secondary pinnae obtuse and frequently their segments also; veins directed both into teeth and into emarginations. *Sori* round, discrete to occasionally overlapping; indusium ovate-lanceolate, frequently with lacerate apex, with elongate cells, provided with scattered unicellular glands (primarily toward base); spores dark brown, echinate, size 38-48 μ. Chromosome number n = 126. (Plate 13)

Distribution. Quebec and Newfoundland, west through the Great Lakes region to Wisconsin.

Type. "Limestone-conglomerate cliffs, headland north of Baptiste Michaud's, Bic, Rimouski Co., Quebec." *Fernald & Collins,* July 18, 1904. (GH!).

Discussion. This plant was recognized by Fernald (Weatherby, 1926) as distinct from *Cystopteris fragilis* var. *fragilis* by its greater size and blunt pinnules, features which he states gives it in the field the aspect of a *C. bulbifera* without the long apex of the frond.

Cystopteris × *laurentiana* appears to be a hybrid between *C. fragilis* and *C. bulbifera*. A discussion of it appears in the section on "Hybridization" above.

It is interesting to note that *Cystopteris* × *laurentiana* has been reported only from regions within the ranges of the tetraploids *C. fragilis* var. *fragilis* and the apparent introgressant "*C. fragilis* var. *mackayi*." It

has not as yet been found in regions occupied by *C. protrusa* which is a diploid.

The resemblance of this hybrid to *Cystopteris fragilis* is so close that it is sometimes difficult to distinguish the two plants. In northern Michigan it often occurs, however, with a wealth of bulblets on the abaxial blade axes. These Michigan populations have been described by Wagner and Hagenah (1956). Unfortunately, over a large part of its range, bulblets occur only rarely. In such cases the diagnostic features are primarily the presence of scattered glands on the indusium, the nature of the vein endings, and the usually large plant, and a spore size within the 6n range.

3. *Cystopteris* × *alpina* (Wulfen) Desv. (pro. spec.).

Polypodium alpinum Wulfen, ex Jacq. Collect II, 171. 1788.
Aspidium alpinum Sw. in Schrad. Journ. d. Bot. 1800, II. 42.
Cyathea alpina Roth, Tent. Fl. Germ. III. 99. 1800.
Cystopteris alpina Desv. Mém. Soc. Linn. Paris, 6: 264. 1827.
Cystea alpina Sm. Engl. Fl. 4: 291. 1828.
Cystopteris fragilis var. *alpina* Koch, Syn. Fl. Germ. Ed. 2. 980. 1845.
Cystopteris fragilis subsp. *alpina* (Wulfen) Hartm. Excurs. Fl. 152. 1846.
Cystopteris fragilis × *montana* Christ, Farnkr. d. Schweiz, 162, f. 28. 1900.

Rhizome short creeping, internodes short with leaves tufted near apex, apex invested with ovate lanceolate scales. *Stipe* stramineous to dark brown, frequently approaching length of blade. *Blade* tripinnate to quadripinnatifid, ovate-lanceolate, up to 21 cm. long and 7.5 cm. wide; minor axes with scattered multicellular glandular hairs; basal pinna pair mostly shorter than succeeding pair, ovate; secondary and tertiary pinna axes winged, the ultimate lobes having either teeth or emarginations commonly with unsymmetrical lateral lobes; veins running into both teeth and emarginations. *Sori* round, discrete; indusium ovate to lanceolate, glabrous, with attenuate cells; spores dark brown, echinate, size 38-48 μ. Chromosome number n = 126. (Plate 14)

Distribution. Mountainous regions of central Europe.

Type. Not seen.

Discussion. This plant is probably the most distinct of the elements which has been attributed to *Cystopteris fragilis* in Europe. This is shown by the relative uniformity in the synonymy. *Cystopteris* × *alpina* resembles *C. fragilis* in the majority of the diagnostic features and thus it is not surprising that past workers have placed it in infraspecific categories of the latter species. The dissection of the blade and the presence of some veins which are directed into emarginations are the only obvious characters which indicate the parentage of *C. montana*. The hexaploid spore size of *C.* × *alpina* also lends to the hypothesis of hybrid origin. These problems have been discussed in the section on hybridization.

The conception of *Cystopteris fragilis* × *montana* Christ is based entirely on the original description and figure by Christ. It is deemed important, however, to bring a consideration of this plant into the broad taxonomy of the genus *Cystopteris* because an intermediacy between *C*

fragilis and *C. montana* appears to exist. In the present treatment this plant is considered to be synonymous with *C.* × *alpina* although different genome combinations may be involved.

An examination of the original description brings one to the conclusion that features characteristic of *Cystopteris fragilis* are of somewhat more importance than those of *C. montana.* The claim of *C. montana* to parentage here lies primarily on the length of the stipe which is the same as the blade and on the basal pinnae which are the longest on the blade. Christ also states that the minuteness and distribution of the sori is similar to that in *C. montana. Cystopteris fragilis,* on the other hand, is represented by characters such as a short rhizome, pinnules with short toothed lobes and veins running into the tips. Thus this proposed hybrid, while it is made quite plausible by the description and figure, needs more study before a decision is made as to its authenticity.

4. *Cystopteris* × *kansuana* C. Chr. (pro. spec.).

Cystopteris kansuana C. Chr. Journ. Wash. Acad. Sci. 17: 499. 1927.

Rhizome short creeping, with leaves tufted near apex, scales clathrate, ovate-lanceolate, sparse. *Stipe* length nearly equal to length of blade, castaneous, delicate. *Blade* bipinnate, lanceolate, tapering to a caudate apex, up to 8 cm. long and 2 cm. broad; primary pinnae opposite to somewhat alternate, distant, ovate, short petiolulate; basal pinnules unequilateral, pinnules with veins extending into emarginations. *Sori* round, discrete; indusium linear, with attenuate cells, glabrous; spores immature but appear aborted. (Plate 19)

Distribution. Type locality.

Type. La Chang K'ou, near Sining, Kansu province, China. *Ching 631.* (US!).

Discussion. This plant is considered to be a hybrid (apparently sterile) between *Cystopteris fragilis* and *C. sudetica* var. *moupinensis* because of the apparent combination of characters of these two species in *C.* × *kansuana.* It possesses the relatively compact rhizome and the blade shape of *C. fragilis.* However, it shows the vein position and the clathrate scales of *C. sudetica* and its related Asian taxa.

5. *Cystopteris diaphana* × *fragilis* complex

Cyathea regia Forster, Sym. Syn. 194. 1798.
Aspidium regium Sw. Schrad. Journ. 1800 (2): 41. 1801.
Nephrodium tenue Michx. Fl. Bor. Am. 2: 269. 1803.
Athyrium regium Spreng. Anleit 3: 139. 1804.
Aspidium tenue (Michx.) Sw. Syn. Fil. 58. 1806.
Athyrium tenue (Michx.) Presl, Rel. Haenk. 1: 39. 1825.
Cystopteris regia (Sw.) Desv. Mem. Soc. Linn. Paris 6: 264. 1827.
Cystopteris tenuis (Michx.) Desv. ibid. 263.
Cystea regia (For.) Sm. Eng. Fl. Ed. 2. 4: 289. 1828.
Cystopteris fragilis B *alpina* var. *regia* Milde, Sporenpfl. 69. 1865.

Cystopteris fragilis var. *mackayii* Lawson, Fern Fl. Can. 233. 1889.
Cystopteris filix-fragilis var. *tenuis* (Michx.) Farwell, Ann. Rep. Mich. Acad. Sci. 6: 200. 1904.
Cystopteris filix-fragilis var. *mackayii* (Lawson) Farwell, Am. Fern. Journ. 27: 14. 1937.

Distribution. Widespread, occurring both where the ranges of *C. fragilis* and *C. diaphana* are in close proximity as well as at some distance from the parents.

Discussion. I believe that all of the synonyms listed above represent intermediates of one form or another between the two extremes *C. diaphana* and *C. fragilis*. The genotypes of these species are presumably similar, or once were similar in the past, in their composition (as might be suspected also on the basis of their similar aspect), for not only where the ranges of the two species are in contact is there evidence of intergradation, but the intergrades are evidently sufficiently viable that they often occur separate from the parents. The assumed exchange of genetic material, therefore, does not appear to have any effect on fertility of the offspring. All *C. fragilis* known today is polyploid; the diploid still remains only in *C. diaphana*, and this species also has 4X and 6X forms. The apparent intermediates are all 4X or 6X, according to spore size.

The expression of this apparent introgression may be observed in three contrasting characters which correlate well in specimens of each species. They are vein position, shape of adaxial epidermal cells and shape of the indusium and its cells.

The putative introgressant individuals exhibit no apparent correlation in regard to the diagnostic characters. Each character seems to be independent of the others and to be expressed in varying ways in different plants.

Accurate taxonomic designation of these apparent introgressants is difficult when one is dealing with large collections. Ideally one should indicate in an annotation the degree of expression of a given species in the introgressant plant. However, the only macroscopic character which may be readily used for this purpose is the vein position. One would then be accused of using "one-character taxonomy" without regard for the expression of the other characters. In practically all examples I studied, evidence of intermediacy in the other characters that separate *C. diaphana* and *C. fragilis* were found. I believe, therefore, that vein position is a reliable indicator of intermediacy.

I have made no attempt to express the relative degree of parental expression but have used the only nomenclatural device that I could in this unusual situation, namely to use the blanket formula *Cystopteris diaphana* × *fragilis*. All of the introgressant plants have the veins entering both teeth and emarginations but in varying ratios.

Since the completion of the foregoing work, new cytological evidence suggests that there may be another interpretation possible for "*C. fragilis* var. *mackayii*" which is a tetraploid. This evidence, obtained by Warren H. Wagner Jr., suggests the possibility that *Cystopteris fragilis* var. *mackayi* may be an ancient segregate resulting from hybridization between two diploid species such as *C. diaphana* and *C. protrusa*. The difference in genome composition may thus explain the ability of "*mackayi*" to maintain its distinctness even when occurring in close proximity to *C. fragilis*, a situation which exists in the extreme northeastern United States and in southeastern Canada.

6. *Cystopteris diaphana* × *protrusa* complex

Distribution. Throughout most of the range of *Cystopteris protrusa*.

Discussion. Apparent introgressant specimens have been observed through the range of *Cystopteris protrusa*. Characteristics of these plants are similar to those described in the above discussion of *C. diaphana* × *fragilis* with the difference that here we are dealing with diploid plants instead of the tetraploid and hexaploid populations of *C. diaphana* × *fragilis*.

SUMMARY

1. The history of the fern genus *Cystopteris* shows that the interpretation of inter-relationships of its species and varieties presents many problems. To contribute to the solution of these problems, this investigation was made, utilizing a number of techniques designed for obtaining and correlating new morphological, anatomical, and cytological data.

2. Spore studies in the genus revealed three general types of spore architecture which correlate closely with the taxonomic delimitation of subgenera. One of these spore types has not been illustrated previously, and intermediate forms were noted between the other two types for the first time.

3. The sizes of spores were found to correlate closely with levels of polyploidy, and thus it was possible to estimate chromosome numbers in the genus where actual counts were not feasible.

4. Preliminary studies of gametophytes indicated differences which may prove to be of taxonomic significance in the future when more extensive surveys are made.

5. Analysis of various anatomical features of the mature sporophytes revealed many new facts which bear on interspecific relationships. The

structures which proved most important were the rhizome scales, the adaxial cells of the leaf epidermis, the laminar trichomes and the indusium.

6. Cytological investigations by previous workers and the present investigator show that there are four polyploid levels in the genus. Three of the chromosome numbers found in this study involve taxa never before reported, and previous findings for a number of species are confirmed by new observations.

7. The role of interspecific hybridization in creating variation in *Cystopteris* has been examined, and it is shown that two mechanisms may be involved, namely allopolyploidy and introgression. Both are believed to account for the traditionally confused concept of the members of the "*Cystopteris fragilis* complex."

8. The world distribution of the members of this genus was determined, and explanations are suggested for the current disjunct distributions of certain of the taxa.

9. Evolution and relationships within the genus were postulated on the basis of a correlation of twelve characters. The species were plotted on a concentric chart using those nine characters which could most readily be assessed as advancements. The position of the species on the chart suggests their probable derivations and groups them according to their common ground plans.

10. As a result of these studies, a taxonomic revision is proposed which divides the genus *Cystopteris* into two subgenera, one of them with two sections. Included is a key to the divisions of the genus and to the ten species which are recognized. Descriptions and discussions of each of the species as well as their probable hybrids are presented, with figures to depict their technical characters.

ACKNOWLEDGMENTS

I wish to express my appreciation for the sustained interest of Dr. Warren H. Wagner Jr. under whose direction this study was undertaken. Mr. Conrad V. Morton of the U. S. National Museum kindly followed my research with interest and gave invaluable assistance in obtaining living plants from various regions of the world. To Mr. Dale J. Hagenah of the Cranbrook Institute of Science I am indebted especially for the knowledge of spores that he imparted on the basis of his own studies.

The following individuals have contributed living specimens and spores for the conduct of this investigation: Mrs. Kathryn E. Boydston, Niles, Michigan; Mr. Garth Brownlie, Christchurch, New Zealand; Professor John E. Cantlon, Michigan State University; Dr. Edward F. Castetter,

University of New Mexico; Mr. Jose Diem, Villa La Angostura, Argentina; Dr. F. Ehrendorfer, Universitat Wien, Austria; Mr. Eugene Horner, Hawaii National Park; Dr. S. Kurata, Tokyo University, Japan; Dr. Jorge Leon, Turrialba, Costa Rica; Dr. Gualterio Looser, Santiago, Chile; Professor E. Matuda, Herbario Nacional del Instituto d'Biologia, Mexico City; Dr. Ronald McGregor, University of Kansas, Lawrence; Dr. H. Merxmüller, Munchen, Germany; Mr. Makoto Nashida, Chiba, Japan; Dr. Josef Poelt, Munich, Germany; Rev. J. F. Smith, Suffield, Connecticut; Mr. Per Stormer, University of Oslo, Norway; Mr. Kakuo Uno, Okayama-ken, Japan; Mr. Harry H. Vannorsdall, Wilmington, Ohio; Professor Cesar Vargas, Cuzco, Peru; Dr. P. Villaret, Lausanne, Switzerland; Dr. Hubert W. Vogelmann, University of Vermont, Burlington; Professor Edgar T. Wherry, University of Pennsylvania, Philadelphia.

Grateful thanks are due to the curators of the herbaria who loaned specimens for this investigation. These herbaria, together with the standard abbreviations as proposed by Lanjouw and Stafleu (1956), were the following:

GH	Gray Herbarium of Harvard University, Cambridge, Massachusetts.
L	Rijksherbarium, Nonnensteeg, Leiden, Netherlands.
P	Museum National d's Histoire Naturelle, Paris, France.
PH	Academy of Natural Sciences, Philadelphia, Pennsylvania.
R	Divisao de Botanica do Museu National, Rio de Janeiro. Brazil.
S-PA	Paleobotanical Department, Swedish Museum of Natural History, Stockholm.
TENN	University of Tennessee, Knoxville.
US	U. S. National Herbarium, Smithsonian Institution, Washington, D. C.
WELT	The Dominion Museum, Wellington, New Zealand.

Latin diagnoses were prepared by Professor R. A. Pack of the University of Michigan, Ann Arbor, Michigan.

APPENDIX

List of Specimen Citations

(The herbarium abbreviations are those proposed by Lanjouw and Stafleu 1956)

1a. *Cystopteris fragilis* (L.) Bernh. var. *fragilis*

SELECTED SPECIMENS:

CANADA.—ALBERTA.—Head of Smoky River, *Hollister* 8 (US); Shaganappi, Calgary, *Moodie*, June 21, 1913 (US); Jasper Park, Cabin Creek, *Macoun* 98124 (US); Rosedale, *Moodie* 987 (US); Waterton Lakes National Park, Waterton, *Hermann* 13078 (US); Chipewyan, *Raup and Abbe* 4688 (US); Lake Mamawi, *Raup and Abbe* 4400 (S-PA). BRITISH COLUMBIA.—Canyon at Carbonate, Selkirk Mountains, *Heacock*, 2 Jul 1904 (US); Queen Charlotte Islands, *Osgood*, 1900 (US); Upper Ingonika River, Cassiar Dist., *Preble and Mixter* 690 (US); 3 miles SW of Malakwa, *Hermann* 12932 (US); Big Bend Dist., Selkirk Mts., *Shaw* 1002 (PH); Lake Mamawi, *Raup and Abbe* 4400 (S-PA). ELLESMERE ISLAND.—Neyprecht Island, *Stein* 178 (US). LABRADOR.—Killinek Island, *Walker* 755 (PH); Battle Harbor, *Williamson*, 6-13 Aug 1911 (PH); Mugford Island, *Palmer*, 27 Aug 1929 (PH); Ungara, *Turner* 673 (US); West Turnavik, *Bartlett* 2 (US). MANITOBA.—Lake Winnipeg, *Macoun*, Aug 1884. NORTHWEST TERRITORIES.—District of Mackenzie, Yellowknife, *Cody and McCanse* 3559 (US); Port Radium, Great Bear Lake, *Shacklette* 2900 (US); District of Franklin, Frobisher Bay, Sylvania Grinnell River, *Collins* 43a (US); Melville Peninsula, Ross Bay, *Cody* 1512 (US). ONTARIO.—0.5 mi. S of Bond Lake, York Co., *Soper and Dale* 4149 (US); Lookout Ridge, Algonquin Park, *Wherry*, 26 Aug 1934 (PH); Batchawa Falls, Algoma district, *Taylor et al.* 170 (S-PA); Rockliffe near Ottawa, *Malte*, 7 Aug 1923 (S-PA). QUEBEC.—Pointe Rouleau, Lake Mistassini, *Rousseau and Rouleau* 663 (US); Grand Cascapedia, Gaspe, *Hart* 12 (US); SW of Bic, Rimouski Co., *Clausen and Trapido* 2836 (US). SASKATCHEWAN.—Lake Athabaska, Charlote Pt., *Raup* 6234 (S-PA). YUKON.—Moosehide Mt., Dawson, *Calder* 2964 (US); Woodchopper Creek, *Collier* 102 (US); 50 mi. above Stewart River, *Tarleton* 151 (US); SE of Lewis, White Pass and Yukon R.R., *Schmid* 48 (PH); Rampart House, Yukon-Alaska Border, *Loan* 693 (S-PA).

GREENLAND.—Head of Söndre Strömfjord, *Erlanson* 2420 (US); Cape Hatherton, *Kodz* 201 (US); Scoresby Sund, *Hartz*, 16 Aug 1891 (US); Kaiser-Franz-Josephs-Fjord, *Buchenau*, Feb. 1895 (US); Godhavn, Kleist, 16 Aug 1904 (S-PA, US); Qagssiarssuk, *Porsild*, 10 Aug 1925 (US); Etah, *Ekblaw* 12 (US); Englishmen's Harbor, Disco Island, *Erlanson* 2870 (US); Grant Fjord off Clavering Fjord, *Bartlett* 429 (TENN, US); Ymerön, Mt. Celsius, *Jarvik*, 31 Jul 1947 (S-PA); Umanak, *Ekman*, 30 Aug 1923 (S-PA); Regio Julianehaab, *Lagerkranz*, 6 Sep 1946 (S-PA); Regio Angmagssalik, *Lagerkranz*, 28 Jul 1946 (S-PA).

GUATEMALA.—Dept. of Huehuetenango, vicinity of Chemal, *Steyermark* 50263 (US); Vicinity of Tunima, *Steyermark* 48411 (US).

ICELAND.—Reykjavik, *Seamman* 1207 (US); Kjosarsysla, Hvalfjordur, Byrnjudalsarfoss, *Lore, A. & D.*, 13 Sep 1948 (S-PA); Hofsfjall, *Davidsson*, 14 Aug 1897 (S-PA); Sedisfjord, *Kjellberg*, 26 Jun 1915 (S-PA); Siglufjord, *Lagerkranz*, 4 Aug 1928 (S-PA).

MEXICO—CHIAPAS.—Acotepec, *Rovirosa* 1054 (PH). COAHUILA.—Villa Acuna, *Wynd & Mueller* 521 (US). GUERRERO.—West of Petlacala, *Mexia* 9068 (US). MICHOACAN.—Vicinity of Uruapan, *Leeds* 231 (PH, US). MORELOS.—Cuernavaca, *Dean*, 7 Jul 1900 (US). PUEBLA.—Popocatepetl, *Rose & Hay* 5989 (US).

UNITED STATES.—ARIZONA.—Coconino Co.: Oak Creek Canyon, *Phillips* 2968

(US). Gila Co.: Workman Creek, *Little* 4301 (US). Pima Co.: Mt. Lemmon, Tucson, *Shreve*, 1 Oct 1917 (S-PA). CALIFORNIA.—Alpine Co.: Pigeon Flat, *Hoover* 5355 (US). Amador Co.: Elsie's Creek, *Hansen* 1460 (US). Butte Co.: Iron Canon, *Austin* 1866 (US). Calaveras Co.: Moran Creek, *Ranzoni*, Aug 1946 (US). Inyo Co.: Sierra Nevada, *Coville & Funston* 2127 (US). Lassen Co.: Susanville, *Jones*, 25 Jun 1897 (US). Madera Co.: Bass Lake, *Storer* 235 (US). Mono Co.: Potato Creek, *Alexander & Kellog* 4516 (US). Nevada Co.: Donner Pass, *Heller*, 17 Aug 1903 (US). Plumas Co.: Lassen Forest, *Eggleston* 7236 (US). San Bernardino Co.: San Bernardino, *Vasey*, Aug 1880 (PH). San Diego Co.: Smith Mt., San Diego, *Orcutt*, Jul 1882 (PH). Santa Clara Co.: Congress Springs, near Saratoga, *Pendleton* 1348 (US). Shasta Co.: Hat Creek, *Hall & Babcock* 4267 (S-PA). Tulare Co.: N of Mineral King, *Wherry*, 23 Jun 1940 (PH). Tuolumne Co.: Eagle Meadow, *Hoover* 1529 (US). COLORADO.—Clear Creek Co.: Berthond Pass, near Georgetown, *Sheldon* 244 (US). Douglas Co.: Franktown, *Wherry*, 17 Jun 1937 (PH). El Paso Co.: W of Palmer Lake, *Wherry*, 26 Jun 1937 (PH). Garfield Co.: trail to Flat Top, *Hermann* 5538 (PH). Gilpin Co.: Tolland, *Palmer* 31392 (S-PA). Gunnison Co.: NW of Crested Butte, *Wherry*, 17 Jul 1937 (PH). Hinsdale Co.: Spring Creek Rd., 8½ mi. S of Pass, *Wherry*, 13 Jul 1937 (PH). Larimer Co.: 9 mi. S of Estes Park, *Benner* 7737 (PH). Mineral Co.: Wagon Wheel Gap, *Wherry*, 12 Jul 1937 (PH). Ouray Co.: Box Canyon, Ouray, *Wherry*, 18 Jul 1937 (PH). Rio Grande Co.: opposite Del Norte, *Wherry*, 12 Jul 1937 (PH). CONNECTICUT.—New Haven Co.: New Haven, *Allen*, 1 Jun 1878 (US). IDAHO.—Bear Lake Co.: Montpelier, *Wherry*, 17 Jun 1931 (PH). Blaine Co.: 5 mi. N of Ketchum, *Henderson* 3264 (US). Boise Co.: on Lowman-Atlanta Rd., *Hitchcock & Muhlick* 10046 (US). Custer Co.: Ryan Peak, *Hitchcock & Muhlick* 10587 (US). Elmore Co.: 10 mi. W of Featherville, *Hitchcock & Muhlick* 10368 (US). Idaho Co.: Heaven's Gate, *Jones, Q.* 218 (US). Latah Co.: Thatuna Hills, *Dillon* 576 (S-PA). Nez Perees Co.: valley of Peter Creek, *Sandberg et al.* 1047 (S-PA, US). Owyhee Co.: East Bruneau, *Nelson & Macbride* 1905 (S-PA, US). Valley Co.: Brundage Mt., *Davis* 2927 (PH). MAINE.—Hancock Co.: Mt. Desert Island, *Wherry*, 21 Aug 1935 (PH). MASSACHUSETTS.—Worcester Co.: Mt. Wachusett, Princeton, *Collins*, 17 Jul 1893 (US). MICHIGAN.—Keweenaw Co.: Lake Bailey, *Hermann* 7739 (US). MINNESOTA.—Lake Co.: East Beaver Bay bluff, *Lakela* 13577 (US). MONTANA.—Gallatin Co.: Lone Mt., Bozeman, *Blankinship* 640 (PH). Lake Co.: Mission Mts., *Kirkwood* 1001 (US). Madison Co.: Devil's Lane, Gravelly Range, *Hitchcock & Muhlick*, 19 Jul 1945 (PH). Meagher Co.: Little Belt Mts., near the Pass, *Flodman* 15 (US). Missoula Co.: O'Keefe's Canyon, near Missoula, *MacDougal* 211 (US). Park Co.: Livingston, *Scheuber*, 10 Jul 1901 (US). Sweet Grass Co.: Wreck Creek, *Eggleston* 7979 (US). NEBRASKA.—Dawes Co.: Belmont, *Webber* 230 (US). Thomas Co.: near Plummer Ford, Dismal River, *Rydberg* 1452 (US). NEVADA.—Clark Co.: Charleston Mts., Little Falls, *Clokey* 8255 (S-PA, TENN, US). Elko Co.: Ruby Mts., *Train* 337 (US). NEW MEXICO.—Grant Co.: Hillsboro Peak, *Metcalfe* 1201 (US). San Miguel Co.: Las Vegas, *Vasey*, Jul 1881 (US). Sierra Co.: Animas Canyon, *Pilsbry*, 10-18 Sep 1915 (PH). NORTH DAKOTA.—Benson Co.: Fort Totten, *Bergman* 1903 (US). Golden Valley Co.: Sentinel Butte, *Clausen* 8217 (US). OKLAHOMA.—Cimmaron Co.: Kenton, *Stevens* 496 (US). OREGON.—Hood River Co.: Mt. Hood, Mirror Lake, *Thompson* 3578 (S-PA). Jackson Co.: near Ashland, *Applegate* 2179a (US). Klamath Co.: Crater Lake National Park, *Coville* 1380 (US). Lake Co.: Lake Albert, *Eggleston* 7145 (US). Union Co.: Lake Anthony, *Wherry*, 3 Jul 1931 (PH). Wasco Co.: Dalles of Columbia River, *Eaton, D. C.*, n.d. (PH). PENNSYLVANIA.—Beaver Co.: Dutchmans Run, *Shafer*, 9 Jul 1885 (PH). SOUTH DAKOTA.—Lawrence Co.: Little Spearfish Canyon, *Over* 13840 (PH). Meade Co.: Piedmont and Little Elk Creek, *Rydberg* 1198 (US.) Washabaugh Co.: Bear Creek, *Over* 1681 (US). UTAH.—Beaver Co.: east of Beaver, *Pennell et al.* 22827 (PH). Duchesne Co.: Mt. Emmons, *Hermann* 5092 (PH). Emory Co.: Wasatch Mts., *Pennell et al.* 22693 (PH). Sanpete Co.: Lake Canyon, Manti, *Tidestrom* 1889 (US). Summit Co.: Lamotte Peak, *Hermann* 5979 (PH). Utah Co.: Provo, *Goodding* 1140 (US). Washington Co.: Pine Valley, *Pennell & Schaeffer* 21826 (PH). WASHINGTON.—

Chelan Co.: Blewett Pass, *Thompson*, 28 Apr 1940 (PH). Clallam Co.: Olympic Mts., *Elmer* 2812 (US). Douglas Co.: Egbert Spring, *Sandberg & Leiberg* 351 (US). Kittitas Co.: Mt. Stuart, *Elmer* 1219 (US). Stevens Co.: Mt. Carleton, *Kreager*, 18 Jul 1902 (US). Whitman Co.: Rock Lake, *Beattie & Lawrence*, 28-30 May 1904 (PH). Yakima Co.: Cleman Mt., *Thompson*, 28 Apr 1940 (PH). WISCONSIN.—Door Co.: Egg Harbor, *Schnatten*, Jul 1882 (US). Iron Co.: Hurley, *Random*, 30 May 1896 (US). WYOMING.—Albany Co.: South Sybille, *Nelson* 7374 (US). Big Horn Co.: South Paintrock Creek, *Williams* 3146 (US). Crook Co.: 5 mi. N. of Sundance, *Porter* 5358 (PH). Fremont Co.: W of Lander, *Porter* 5588 (PH, US). Johnson Co.: near Buffalo, S Fork of Clear Creek, *Williams*, 3 Aug 1898 (US). Lincoln Co.: Afton, *Payson & Armstrong*, 24 Jun 1923 (PH). Teton Co.: Hoback Canyon, *Porter* 1157 (S-PA). Washakie Co.: upper Lee Creek, Big Horn Mts., *Pennell & Shaeffer* 24330 (PH). ALASKA.—Sadlerochit River, *Spetzman* 1184 (US); Nome, *Flett* 1508 (US); Mitrofania Bay, Alaska Peninsula, *Griggs*, 20 Jul 1913 (US); Umiat, Colville River, *Spetzman* 2205 (US); Lake Peters (E of Canning River), *Spetzman* 1402 (US); Yakutat, *Stair*, 14 Jul 1945 (PH); Rapids Lodge, 138 mi. S of Fairbanks, *Scamman* 4 (S-PA). Aleutian Islands: Dutch Harbor, Unalaska, *Flett* 1517 (US); Glacier Valley, Unalaska, *Jepson* 250 (US); Great Sitka, *Llano* 1194b (US); Attu Island, *Llano* 1393a (US); False Pass, Unimak Island, *Eyerdam* 2111 (S-PA). Pribilof Islands.: St. Paul Island, *Palmer* 181 (US); St. Paul Island, *True & Prentiss* 41 (US); St. George Island, *True & Prentiss* 61 (US).

ASIA (INCLUDING SOVIET UNION)

AFGHANISTAN.—Kurrum Valley, *Aitchison*, Dec 1879 (S-PA).

CEYLON.—Sudspitze, *Smith* (S-PA).

CHINA.—Kansu.: Lan Ze Cheon K'ou, near Sining, *Ching* 592 (US). Shansi.: Cich-hsiuh district, Cho-mei-shan, *H. Smith*, Oct 1924 (S-PA); Yuan-chu district, Ye-cho-shan, *H. Smith*, 18 Jul 1924 (S-PA). Sinkiang.: Bogdo, Fu-Shn-Shan, *Hummel*, 15 Jun 1928 (S-PA); Bogdo, Ozun-ava, *Hummel*, 7 Jun 1928 (S-PA). Szechuan.: Karlong, *Smith*, 3 Aug 1922 (S-PA); Tsipula, *Smith*, 26 Aug 1922 (S-PA); Dongrergo, *Smith*, 9 Aug 1922 (S-PA); Hsioch-shan, *Smith*, 19 Jul 1922 (S-PA). Thibet: Ladak, Dah, *no coll.* (S-PA); Balti, Skardo, *no coll.* (US).

JAPAN.—Hondo, Azusayama, in Shinano, *Ohwi* 249 (L, S-PA, US); Sakhalin Island, Mereyo, *Faurie* 305 (S-PA); Shinano, Mt. Toyoguchi, *Hamegata* 3439 (US).

IRAN.—Kuhikakaghan, Mazenderan, *Koelz* 16386 (US); Dimalu, Mazenderan, *Koelz* 16551 (US); Bardu Forest, Khorassan, *Koelz* 16762 (US); Kerman province, Kerman, *Bornmuller* 4487 (PH).

IRAQ.—Arl Gird Dagh, *Gillett* 12357 (US); Sefin Dagh, *Gillett* 8152 (US); Ser Kurawa, *Gillett* 9771 (US).

MONGOLIA.—Honger obbo, *Eriksson* 281 (US); Kentei Mts., at source of Tola, Mensa and Iro rivers, *Ikonnikov-Galitzky*, 1 Aug 1929 (S-PA); Ara-Khangai district, Khanchai, *Nabrob*, 3 Aug 1926 (S-PA).

INDIA.—Simla, *Collett*, Oct 1885 (S-PA). KASHMIR.—Bok, Zanskar, *Koelz* 2964 (L, S-PA); Ka La, Ladak, *Koelz* 2508m (L); Gilgit (Balti or Little Tibet), *Winterbottom*, 8 Aug 1847 (L); Srinagar, Tangmarg, *Hummel*, 29 Mar 1953 (S-PA); Gulmarg, *Stewart*, 26 Jul 1926 (PH); Padam, Zaskar, *Koelz* 5750 (US); Mune, Zaskar, *Koelz* 5730 (US); Pahlgam, *Stewart* 21897B (US); Pensi La, Zanskar, *Koelz* 2934k (US); Tragbal, *Stewart* 4719 (US); Sonamiarg, *Stewart* 3461 (US).

PAKISTAN.—Swat, between Maina and Ham Mts., *Rodin* 5469 (US); Lahul, Kangra, *Koelz* 5190 (US); Sisu, Lahul, *Koelz* 648 (US); Changla Gab, Murree Hills, *Stewart* 4061a (US); Chamba, Saeh Pass, *Stewart* 2610 (US); Chamba, Alwas, *Stewart* 2420 (US); Chitral, Lowari Pass, *Harriss* 16885 (S-PA); Chitral, Barum Gol, above Shokor Shal, *Wendelbo*, 19 Jun 1950 (S-PA).

UNION OF SOVIET SOCIALIST REPUBLICS.—Azerbajdzhan, Caucasus Mts., *Karjagin*, 26 Jul 1935 (US); Caucasus, Stavropol, *Noropokrorsky & Turkevicz*, 26

Jun 1915 (S-PA); Tiflis (Tbilisi), *Kousnetzoff*, 18 Jul 1890 (S-PA); Caucasus, Majkop, *Meemynoh*, 27 Aug 1911 (S-PA); Armenia, near Lemenowka, *Fomin*, 4 Jul 1929 (S-PA); Ukraine, Czerkassy, Korsua, *Pidophiezka*, Jul 1924 (S-PA); Karelia, *Hulten*, 29 Jun 1927 (S-PA); Moskau, *Ziekendrath*, 29 Jun 1900 (S-PA); Moscau, Kunzewo, *Ziekendrath*, 26 Sep 1894 (S-PA); Ingricae [between Lake Lodoga & Lake Peipus], *Borisova*, 6 Jul 1927 (S-PA); Estonia, between Keila and Joa, *Lundstrom*, Jul 1922 (S-PA); Latvia, Vidzeme, Priekuli, *Starcs*, 25 Aug 1924 (S-PA); Konigsberg, Frederickstein, *Baenitz*, 6 Aug 1881 (S-PA); Pskow, near river Welikaja, *Andrejew*, 30 Aug 1900 (S-PA); Tomsk, Zmeinogorsk, *Iljin*, 29 Jun 1909 (L); Semipalatinsk, *Schipczinsky*, 19 May 1914 (S-PA); Altai, Buchtarminsko, *Meyer*, n.d. (S-PA); Zabaikalski, Mangischlak-halvon, *Dubianskii*, 8 May 1906 (S-PA); Schilka [Transbaikal], *Turszaninow*, n.d. (S-PA); Songarei, Alatan, *Schrenk*, 6 Jun 1842 (S-PA). Vladimir, Kardbanowo, *Ziekendrath*, 25 Jun 1894 (S-PA); Regio transiliensis (Vjernyi district, near lake Issyk), *Titov*, 13 Sep 1915 (S-PA); Charkov, Zmievsk, *Miljotin*, 13 Jul 1912 (S-PA); Nova Zemlia, sinus Karmakulski, *Ekstam*, 16 Aug 1901 (S-PA); Nova Zemlia, Mal. Kaimakul, *Ekstam*, 3 Sep 1901 (S-PA); Nova Zemlia, Machiggin, Blomstre, *Lyrge*, 3 Aug. 1921 (S-PA). SIBERIA.—Jakutsk, Bulun, *Nilsson*, 1898 (S-PA); Jakutsk, Kumach-Sur, *Nilsson*, 24 Jul 1898 (S-PA); Jakutsk, Balaganach, *Nilsson*, 27 Jun 1898 (S-PA); Jenisei, Stolba, *Arnell*, 1 Jul 1876 (S-PA); Jenisei, Mjelnitza, *Brenner*, 12 Jul 1876 (S-PA); Jenisei, Uskimys, *Arnell*, 5 Jul 1876 (S-PA); valley of river Lena, Natara, *Nilsson-Ehle*, 22 Jun 1898 (S-PA) KAMCHATKA.—Bogatyrjovk (Avatscha Bay), *Hulten*, 16 Jul 1920 (S-PA); Cape Koslof, *Malaise*, Jun 1923 (S-PA); Unkanaktjeks, Golyginas flodsystem, *Hulten*, 20 Aug 1922 (S-PA). KURIL ISLANDS.—Paramushir Tokari, *Bergman*, 5 Sep 1930 (S-PA).

TURKEY.—Zudschias Dagh, *Cyren*, 4 Jun 1927 (S-PA); Bithynisha Olympen, *Cyren*, 15 Jun 1927 (S-PA); Cilicico-Kurdicum, Karduchia, Mukus, *Kotschy*, Sep 1859 (S-PA); Anatolis, *Wiedermann*, n.d. (S-PA).

EUROPE (EXCLUDING SOVIET UNION)

AUSTRIA.—Tirol, Braunesk, Leimbach, *Wolf*, n.d. (L.); Badgastein, *Splitgerber*, Jun 1862 (L); Gmunden, *Dorfler*, n.d. (S-PA); Styria, *Agardh*, 1827 (S-PA); Gostling, *Kummerle*, 28 Sep 1905 (S-PA).

BELGIUM.—Namur, Gedinne, *Gravet*, 6 Jul 1884 (L); Malmedy, *Kern*, Aug 1939 (L); Spa, *Thielens*, Aug 1862 (L); Namen, *Thielens*, Aug 1861 (L); Namur, Nafraiture, *Gravet*, 29 Jul 1886 (L); Namur, Ouhimont, *Gravet*, 26 Aug 1867 (L); Dinant, *Gravet*, 10 Jul 1871 (L).

BRITISH ISLES.—SCOTLAND.—S. Aberdeen, Morrone Hill near Braemar, *Hoogland*, 17 Jul 1948 (L); Perth, near Crienlauch, *Hoogland*, 30 Jun 1948 (L); Orkney Islands, Hoy, *Johnston*, 6 Aug 1924 (S-PA).

BULGARIA.—Mt. Vitosa, Zlatni-Mostove, *Vihodzevssky*, 1 Aug 1952 (S-PA).

CZECHOSLOVAKIA.—Bohemia, *Skarnitzl*, 14 Aug 1903 (S-PA); Bohemia, Telsdorf, *Rosendahl*, Jul 1910 (S-PA); Moravia, Brno, *Bily*, 2 Aug 1934 (S-PA).

DENMARK.—Skjor, Boegerbregne, *Möller*, May 1894 (S-PA); Sjaelland Island, *Thomsen*, 4 Jun 1870 (L); Faeroes, Stromo, Kirkebo, Thorshavn, *Feilberg & Rostrup* 16 Jul 1867 (S-PA).

FINLAND.—Aland, Eckero, *Möller*, 16 Jul 1928 (S-PA); Kuusamo, Paanajarvi, *Baekman*, 1 Jul 1902 (S-PA); Sydvaranger, Elvenes, *Norrman*, 2 Aug 1937 (S-PA); Aland, Sund, Bomarsund, *Möller*, 18 Jul 1928 (S-PA); Karelia, Sunku, Arsenovalok, *Sparre*, 5 Jul 1942 (S-PA); Tavastia, Lammi, *Baekman*, Aug 1909 (S-PA).

FRANCE.—Isere, Platernoz, *Milliat & Aines* 214 (P); Puy de Dome, Mont-Dore, *Ozanon*, 26 Jul 1884 (P); Vosges, pres du la cascade de la Serva, *Silbermann*, Oct 1865 (P); Haute-Savoie, Bourguignon-les-Conflaus, *Bertrand*, Aug 1891 (P); Cantal, bois de Messilac, *de Puyfol*, 22 Jun 1889 (S-PA); Drome, foret de Taou, *Gombault*, 24 May 1924 (S-PA); Corsica, Fort Vizzavona *Hemmendorff*, 25 Jun 1924 (S-PA).

GERMANY.—Westfalen, Witten, *Schemmann*, Jun 1907 (L, S-PA); Baden, Heidel-

berg, *Voigtlaender-Tetzner*, 7 Jun 1907 (S-PA); Thuringen, Jena, *Dietrick*, 3 Aug 1832 (S-PA); Sachsen, Zwickau, *Lehmann*, 13 Jun 1902 (S-PA); Neanderthal prope Dusseldorf, *de Vriese*, n.d. (L); Brandenburg, Neuruppin, *Warnosorf*, Jul 1891 (S-PA); Bayern, Oberpflalz, Velburg, *Prechtelsbauer*, Aug 1901 (S-PA); Bayern, Oberstdorf, *Krieger*, Aug 1906 (S-PA).

GREECE.—region of Parnassos Mt., *Guicciardi*, Jul 1855 (L).

HUNGARY.—Posoniensis, *Baumler*, Jul 1911 (S-PA); Lika-Kobava, *Kummerle*, 27 Jul 1929 (S-PA); Tozsony, Tozsony, *Baumler*, May 1878 (S-PA); Szepes, *Filarszky*, Jnl 1906 (S-PA); Gomor, *Richter*, 20 Aug 1898 (S-PA).

ITALY.—Etrusca, NW of Rome, *Maggio*, 1882 (L); Mountains Merano (S. Tirol), *Enander*, 15 Sep 1925 (S-PA); Liguria uber Tenda, *Bicknell*, Jul 1901 (S-PA); Toscana, *Ascherson & Reinhardt*, 19 Jul 1863 (S-PA); Emilia, Modena, *Vaccari*, Aug 1886 (S-PA); Piedmont, Cottian Alps, *Rostan*, 1880 (S-PA); Toscana, Monte Falterona, *Corradi*, 4 Aug 1946 (L); Sicily, Mt. Aetna, *Splitgerber*, 27 May 1833 (L); Sicily, Mt. Aetna, *Huet du Pavillon*, 12 Jul 1855 (L).

LUXEMBOURG.—Berdorf, *van Steenis*, 28 Jun 1924 (L); Echternach, *van Steenis*, 25 Jun 1924 (L); Orval [?], *Gravet*, 18 May 1857 (L).

NETHERLANDS.—Ijsland, Husafell, *de Lange-Luyten*, 27 Jul 1932 (L).

NORWAY.—Kongsvold (Dovre Fjeld), *Baenitz*, 26 Jul-13 Aug 1891 (L); Troms, Salagen, *Norrman*, 10 Aug 1938 (S-PA); Dombas, Hareggur, *Gunnarsson*, 19 Aug 1929 (S-PA); Nordfjorden, *Malmgren*, 10 Aug 1868 (S-PA); Skamberget, *Mattiorit*, 27 Jul 1882 (S-PA); Cap Thorsten, *Nath*, 1870 (S-PA); Isfjorden, Kap Boheman, *no coll.*, 30 Jul 1896 (S-PA); Tempelbay, *Mathorst*, 25 Jul 1882 (S-PA).

POLAND.—Silesia, Gorlitz, *Baenitz*, 1860 (S-PA); Silesia, Breslau, *Callier*, 8 Sep 1925 (S-PA); Elk, *Savio*, 21 May 1888 (L); Danzig, *Klatt*, 3 Jun 1841 (S-PA); Riesengebirge, Agneteudorf, *Tescheow*, Aug 1909 (S-PA).

ROMANIA.—Transsilvania, district of Fagaras, *Buia et al.*, 13 Aug 1936 (S-PA); Transilvania, *Barth*, 6 Jun 1908 (S-PA).

SWEDEN.—Vestrogotland, Toarps, *Olson*, 2 Jun 1914 (S-PA); Torne Lappmark, Abisko, Nuolja, *Rosendahl*, Jul 1910 (S-PA); Ostergotland, Omberg, Alvastra, *Dahlstedt*, 14 Jul 1881 (S-PA); Stockholm, Naska, *Thedenius*, 1852 (S-PA); Jamtland, Froson, *Rosendahl*, Aug 1912 (S-PA); Skaraborg, Smedstorfs, *Thunsee*, 26 Jun 1908 (S-PA); Blekinge, Nattraby, *Arrhenius*, 3 Aug 1927 (S-PA); Oland Island, Borgholm, *Munthe*, 18 Aug 1901 (S-PA); Gotland Island, Ljugarn, *Skarman*, Jul 1895 (S-PA); Smaland, Madesjo, *Medelius*, 28 Jun 1910 (S-PA); Nerike, Palsboda, *Sjoholno*, 1888 (S-PA); Harjedalen, Tannas, *Setting*, 4 Jul 1946 (S-PA).

SWITZERLAND.—Vand, Pont de Nant, *Masson*, Aug 1886 (US); Wallis, Zennalt, *Birger*, 21 Jun 1925 (S-PA); Lugano, *Birger*, 31 May 1925 (S-PA); Berne, Blumenthal, *Rosendahl*, Jun 1903 (S-PA); Wallis, Alpe de Cleuson, *Wolf*, Sep 1904 (S-PA); Grisons (Graubunden), *Hooker*, 1862 (S-PA); Wandt, *Wilczek & Wirtgen*, 19 Aug 1902 (S-PA); Fribourg, between Charmey and Cerniat, *Brunner*, 13 Jul 1950 (L).

JUGOSLAVIA.—Bosnia, Vlasic Plateau, *Brandis*, 23 Aug 1897 (S-PA); Montenegro, Landzak, *Nuravjev*, 8 Jun 1930 (S-PA); Bosniz, Sarajevo, *Murbeck*, 11 Jun 1889 (S-PA); Montenegro, *Rohlens*, n.d. (S-PA).

1b. *Cystopteris fragilis* var. *apiiformis* (Gandoger) C. Chr.

SELECTED SPECIMENS:

NEW ZEALAND.—Upcot, Awateri Valley, Marlbro, *Petrie*, Feb. 1922 (WELT); Bealey, Canterbury, *Kirk*, 1883 (US, WELT); W part of Amurilo, W of Moorison, *Petrie*, n.d. (WELT); Clutha Valley, S from Alexandra, *Petrie*, Nov 1893 (WELT); Upper Waimakariri, South Island, *Kirk*, n.d. (WELT); Isolated Hill, Marlbro, *Alston*, 25 Apr 1915 (WELT); Central Otago, *Petrie*, n.d. (WELT); Castle Hill, *Kirk*, 24 Jan 1891 (WELT); Amuri, *Kirk*, n.d. (WELT); Nelson, *Pant*, n.d. (WELT); Tre-

lisiek, Canterbury, *Kirk*, Jan 1896 (WELT); Mingha Valley, *Oliver*, 15 Jan 1928 (WELT); Otago Province, head of Lake Waikatipu, *Walker* 4688 (US).

ARGENTINA.—Patagonia.: Baguales, *Borge* 102 (S-PA); Tweedie, *Borge* 211 (S-PA); Lago Argentino, *Furlong* 8 (US); Magalhaens Land, *Andersson*, 1852 (S-PA); Nahuel Huapi, *Bachtien*, 14 Feb 1905 (US).

CHILE.—Territory Magallanes, Last Hope Inlet, *Mexia* 7991 (S-PA, US); Aysen province, E of Coihaique, *Correll* C123 (US).

FALKLAND ISLANDS.—Roy Cove, *Skottsberg* 61 (ISOTYPE, S-PA).

SOUTH GEORGIA.—*Mosthaff*, 18 Mar 1883 (S-PA).

KERGUELEN ISLAND.—*Kidder*, 24 Dec 1874 (US); *Kidder*, 10 Dec 1874 (US); *Haumann*, 17 Nov 1874 (US); *Eaton*, 26 Feb 1875 (S-PA).

1c. *Cystopteris fragilis* var. *luteri* Hausman

SPECIMENS EXAMINED:

AUSTRIA.—Tirol.: *Roseustoek*, 29 Sep 1901 (S-PA); *Roseustoek*, 29 Jul 1901 (S-PA); *Rosenstoek*, 27 Jul 1901 (L).

BELGIUM.—Ardennes Mts., Libramont, *Hostie*, 3 Jul 1938 (P).

HUNGARY.—Montes Magas Tatra, *Kummerle & Timko*, 7 Jul 1916 (S-PA).

ITALY.—S Tirol, *Gross*, 19 Jul 1933 (US); Bormio, *Soderlund*, 2 Aug 1921 (S-PA).

SWITZERLAND.—Berne Oberland, Kandersteg, *Tavel*, 14 Aug 1917 (S-PA).

2. *Cystopteris protrusa* (Weath.) Blasdell

SELECTED SPECIMENS:

UNITED STATES.—ARKANSAS.—Logan Co.: Magazine Mt., *Wherry*, 30 Apr 1934 (PH). Washington Co.: N of Fayetteville, *Wherry*, 6 May 1925 (US). ALABAMA.—Tuscaloosa Co.: 8 miles above Tuscaloosa, *Harper* 3047 (PH). GEORGIA.—Rabun Co.: near summit of Black Rock Mt., *Correll* 6617 (US). ILLINOIS.—Champaign Co.: Urbana, *Gates* 1946 (US). Du Page Co.: rich woods near Roselle, *Chase* 9427 (US). Peoria Co.: Princeville, *Chase*, 28 May 1896 (PH). Richland Co.: Bird Haven, near Olney, *Ridgway* 3035 (PH). INDIANA.—Posey Co.: Nash's Woods, *Cain*, 12 Jul 1932 (TENN). Wells Co.: Woods 3/4 miles N of Bluffton, *Deam*, 3 Jul 1907 (PH). IOWA.—Allamakee Co.: S side of Yellow River, *Wherry*, 1 Jun 1937 (PH). Clayton Co.: S of McGregor, *Wherry*, 1 Jun 1937 (PH). Mitchell Co.: 3 mi. SW of Osage, *Wherry*, 2 Jun 1937 (PH). KENTUCKY.—Edmonson Co.: Vicinity of Mammoth Cave, *Palmer*, May 1899 (US). Harlan Co.: Little Black Mt., *McCoy*, 26 Aug 1934 (PH). Kenton Co.: Taylon ravine, *Lea*, 3 Jun 1840 (PH). Madison Co.: E of Berea, *Smith, L. B. et al.* 3604 (US). MICHIGAN.—Oakland Co.: Section 4 Southfield Twp., *Hagenah* 877 (US). Washtenaw Co.: Huron River Drive, Ann Arbor Twp., *Wagner* 8073 (MICH). MISSISSIPPI.—Westside, *Tracy* 1399 (US). MISSOURI.—Marion Co.: Hannibal, Mark Twains' Cave, *Davis*, 9 Jul 1909 (PH). Stoddard Co.: Crowley's Ridge, near Messler, *Palmer* 34847 (PH). NEW YORK.—Richmond Co.: Staten Island, Bloodroot Valley, *Dowell* 3884 (US). NORTH CAROLINA.—Alleghany Co.: near Twin Oaks, *Correll & McDowell* 10821 (US). Avery Co.: ½ mi. S of Cranberry, *Wherry*, 17 Jul 1938 (PH). Buncombe Co.: 3 mi. SE of Beech, *Wherry*, 1 Jun 1939 (PH). Jackson Co.: E of Glenville, *Godfrey & O'Connell* 51976 (US). Oconee Co.: Tomassee Knob, *House* 2092 (US). Swain Co.: Nantahala Gorge, *Leeds* 474 (PH). Transylvania Co.: 5 mi. S of Toxaway Station, *Wherry & McVaugh*, 12 Jul 1936 (PH). Yadkin Co.: near Lime Rock along the Yadkin River, *Correll & McDowell* 10964 (US). OHIO.—Hamilton Co.: ad ripas fluminis Ohio, prope "North Bend," *Short*, n.d. (PH). Lorain Co.: Pittsfield, *Rickseeker*, 5 Jul 1894 (US). PENNSYLVANIA.—Allegheny Co.: *Hatry*, 11 May 1902 (US). Bedford Co.: ½ mi. SW of Sulphur Springs, *Berkheimer* 1254 (PH). Centre Co.: 2 mi. SW of Woodward, *Wahl* 1468 (PH). Dauphin Co.: Harrisburg, *Williamson*, 1 June ? (PH). Greene

Co.: 1¾ mi. E of Waynesburg, *Wherry & Leeds* 3501 (PH). Lycoming Co.: 1 mi. NW of Montoursville, *Wherry*, 2 Jun 1941 (PH). York Co.: York Furnace, Lower Susquehanna River, *Stone*, 19 May 1906 (PH). TENNESSEE.—Bedford Co.: near Normandy, *Shaver* 10455 (TENN). Blount Co.: 1 mile from Kinzel Springs Hotel, *Shaver* 10230 (TENN). Clay Co.: 2.1 mi. W of Celina, *Shaver* 10513 (TENN). Cocke Co.: 16 mi. E of Newport, *Shaver* 10213 (TENN). Coffee Co.: Rutledge Falls near Tullahoma, *Sharp* 4745 (TENN). Franklin Co.: near Suwanee, *Harlow*, n.d. (US). Giles Co.: near Milky Way Farm, W of U.S. 31, *Shaver* 10469 (TENN). Hawkins Co.: E of Kyles Ford, *Shaver* 10212 (TENN). Hickman Co.: 8.1 mi. E from road 100, *Shaver* 9162 (TENN). Knox Co.: Wooded talus slope, Gallagher Ferry, *Shaver* 10494 (TENN). Lewis Co.: 4.1 mi. N of Hohenwald, *Shaver* 10208 (TENN). Lincoln Co.: Teal Hollow, near Kelso, *Shaver* 10450 (TENN). Loudon Co.: limestone bluff by Clinch River, *Shaver* 10500 (TENN). Macon Co.: 5.9 mi. E of LaFayette, *Shaver* 10481 (TENN). Marion Co.: 1 mi. from Ladds Station, *Shaver* 10233 (TENN). Maury Co.: 2 mi. W of Hampshire, *Shaver* 10203 (TENN). Montgomery Co.: Porter's Bluff, *Shanks* 2032 (TENN). Obion Co.: near Reelfoot Lake, *Avery NN28* (TENN). Pickett Co.: 1.9 mi. NW of Forbus, *Shaver* 10509 (TENN). Shelby Co.: Shelby Forest Park, *Sharp* 10415 (TENN). Obion Co.: near Reelfoot Lake, *Avery* NN28 (TENN). Pickett Co.: 1.9 mi. Co.: 2 to 3 mi. S of Watertown, *Shaver* 10488 (TENN). VIRGINIA.—Fairfax Co.: Potomac side, *Langley, Palmer*, 19 May 1901 (PH). Loudoun Co.: 1 to 2 mi. below Harpers Ferry, *Benedict* 2886 (PH). WEST VIRGINIA.—Fayette Co.: 1 mi. N of Gauley Bridge, *Wherry*, 23 Jul 1935 (PH). Grant Co.: 1½ mi. NE of Petersburg, *Wherry*, 12 Apr 1936 (PH). Greenbrier Co.: 1½ mi. SW of Renich P.O., *Wherry*, 20 Jul 1938 (PH). Mingo Co.: 1 mi. N of Nolan, *Wherry*, 12 Jul 1938 (PH). Ohio Co.: 7 mi. E of Wheeling, *MacElwee*, n.d. (PH). Ritchie Co.: Laurel Junction, *Smith*, 12 Sep 1879 (US). WISCONSIN.—Grant Co.: 15 mi. NW of Bloomington, *Tryon & Tryon* 4346 (TENN, US).

3. *Cystopteris douglasii* Hooker

SPECIMENS EXAMINED:

HAWAII.—*Baldwin*, n.d. (PH). HAWAII.—Mauna Kea, n.d. (S-PA); Mauna Kea, *Faurie* 159 (S-PA). KAUAI.—Waimea, *Faurie* 157 (S-PA). MAUI.—Kaleakala Crater, *Wagner* 5261 (UC); Haleakala, *Mann & Brigham* 480 (US); *Lichtenthaler*, n.d. (US); East Maui, *U.S. S. Pacific Expl. Exped.* 1838-42 (US); Haleakala, *Faurie* 158 (S-PA).

4. *Cystopteris montana* (Lam.) Bernh.

SELECTED SPECIMENS:

NORTH AMERICA:

ALASKA.—McKinley National Park, W of Wonder Lake, *Mexia* 2188 (PH); Anchorage, *York* X122 (PH); Teller Reindeer Station, Port Clarence, *Walpole* 1956 (US); Seward Peninsula, W of Kruzgamapa River, *Collier*, 1900 (US); 5 mi. N of Nome City, Fleet 1507 (US); Fort Gibbon, *Heideman* 79 (US); Livengood, about 80 mi. NNW of Fairbanks, *Scamman* 4879 (US); Brooks Range, NW of Walker Lake, upper Kopuk River, *Jordal* 3971 (US); Port Vita, Raspberry Island, Kodiak group, *Eyerdam* 3917 (US); Wiseman, on Middle Fork of the Koyukuk River, *Scamman* 2180 (US); Alaska Range, Healy on west side of Nenana Valley, *Porsild* 317 (US).

CANADA.—ALBERTA.—Lake Louise, *Brown* 711 (PH); Slave Lake District, Atauwan River (Salteau), *Brinkman* 4211 (US). BRITISH COLUMBIA.—Yoho Valley, Selkirk Mts., *Shaw* 586 (PH); Big Bend Highway, near Kinbasket Lake, *Eastham* 9292 (US); Selkirk Mts., woods near Fish Lake, *Shaw* 1210 (PH, US). LABRADOR.—Straits of Belle Isle, Blanc Sablon, *Fernald & Wiegand* 2333 (PH, US); Rama, *Sticker* 374 (US); Attikamagen Lake, Iron Arm, *Harper* 3565 (US). NEWFOUNDLAND.—Straits of Belle Isle, Savage Cove, *Fernald et al.* 26153 (PH, US). ONTARIO.—Royston Park, Owen Sound, *Macoun*, 1876 (PH); Fort William, *Williamson* 2337

(PH); E of Port Arthur, *Williamson*, n.d. (PH). QUEBEC.—Gaspe Co.: trail from the Forks of the River Ste. Anne des Monts to Table-topped Mountain, *Fernald & Collins* 290 (PH); Mt. Albert, *Fernald et al.* 25373 (PH, US); Lake Mistassini, *Rousseau & Rouleau* 856 (US). YUKON.—Klondike, Indian Divide, *Tarleton* 152c (US); Melozi River, *Collier* 135 (US); Dawson, *Eastwood* 453 (US); Canol Rd., Mile 55-60 Quiet Lake, *Porsild & Breitung* 11107 (US).

GREENLAND.—S. f. Kiagtut, Tunugdliarfik-Fjord, 61°10′ N., *Porsild & Porsild*, 10 Aug 1925 (US).

UNITED STATES.—COLORADO.—Sawatch Range, Mt. Antero Spur, *Brandegee*, Jul 1880 (PH, US); Summit Co.: 2 mi. by road N of Hoosier Pass, *Wherry*, 11 Aug 1937 (PH, US). MONTANA.—Gruenight [?] Pass, Glacier National Park, *Rugg*, Jul 1932 (US).

EURASIA:

AUSTRIA.—Voralberg, *Barkman* 3566 (L); Tirol, between Matrei & Kloster, *Hallier*, 30 May 1890 (L); Kärnten, *Rustofry*, 11 Aug 1877 (L); Carinthia, *Hoppe*, n.d. (L); near Gmunden, *Dorfler*, 23 Jul 1888 (L, S-PA); Alps of Salisburg, *Meudil*, n.d. (US); Styria, Murau, *Fest*, Jul 1900 (US).

CHINA.—KANSU.—near Pingfan, *Ching* 572 (US); Ta Hwa, near Pingfan, *Ching* 553 (US); Tai-tong-ho, *Licent*, 19 Aug 1918 (P).

CZECHOSLOVAKIA.—Slovakia, on calcareous cliffs along moist ravines, *Suza*, 13 Jun 1930 (US); Slovakia septentrionalis, montes Bielske Tatry, *Domin & Krajina*, 10 Jul 1929 (PH, US).

FINLAND.—Sakkabani, *Krok*, 11 Jul 1898 (S-PA); Kuusamo, Paanajarvi, *Moutell*, 4 Jul 1898 (S-PA); Lapponia ponojensis, Katschkowka, *Kihlman*, 24 Jul 1889 (S-PA).

FRANCE.—AIN.—Jura Mts., between Faucille and Mijoux, *Machalet*, 10 Aug 1856 (P). DROME.—Lus-la-Croix, *Chatenier*, 26 Aug 1890 (P). HAUTES-PYRENEES.—Cascade de Splumons pres Cauterets, *Vallot*, Jul 1885 (P). ISERE.—Choroland, *Milliat*, 15 Aug 1939 (P).

GERMANY.—near Salzburg, Austria, *Schott*, n.d. (US); Baiern, *Magnus*, 11 Aug 1874 (US); Bavaria, Berchtesgaden, *Ball*, 1890 (US).

HUNGARY.—Csik, near Gyilkosto, *Boros*, 24 Jul 1941 (S-PA).

INDIA.—Kashmir, Sonamarg, *Stewart* 6868 (US); Kumann, Ralam Glacier, *Duthie* 3647 (US); Western Nepal, Budhi Village, *Duthie* 6274 (US).

ITALY.—Mt. Sciliar, above Siusi, NE of Bolzano, *Chrysler* 2895 (PH).

NORWAY.—Dovre, Kongsvold, *Wallin*, 7 Aug 1883 (S-PA); Troms, Gratangen, *Norrman*, 6 Aug 1938 (S-PA); Nordland, Saltdalen, Solvagbind, *Asplud*, 30 Jul 1937 (S-PA); Gudbrandsdalen, Ringsbos, *Zetterstedt*, 22 Jun 1870 (US).

SWEDEN.—Jamtland, Tannforsen, *Rosendahl*, 8 Jul 1910 (S-PA); Angermanland, Tasjo, *Cedergreu*, 13 Jul 1927 (S-PA); Dalarna, Orsa, *Rosendahl*, Jul 1912 (S-PA); Harjedalen, Tannas, *Engstedt*, 31 Jul 1932 (S-PA); Asele Lappmark, Dorotea, *Samuelsson*, 26 Aug 1926 (S-PA); Lyeksele Lappmark, Baeknas, *Nordenstam*, 13 Jul 1936 (S-PA); Pite Lappmark, Arjeplog, *Wistrand*, 13 Jul 1947 (S-PA); Lappland, Jukkasjarvi, Abisko, *Samuelsson & Zander*, 14 Aug 1927 (L, S-PA).

SWITZERLAND.—Unterwalden, between Grasenberg and Engenberg, *Cramer*, Jul 1859 (L); Waadt, *Wirtgen* 329 (L); Vaud, Pays-d'Enhaut, *Villaret*, 17 Aug 1952 (US); Glarus, prope Stachelberg, *Ball*, Jul 1857 (US); Bern, Rosenlani, *Ball*, 12 Aug 1857 (US); Bonavalettaz (Gruyere), *Castella*, 3 Aug 1906 (US).

UNION OF SOVIET SOCIALIST REPUBLICS.—Caucasus, *Busch*, 28 Aug 1933 (PH); Syktyvkar district, Komi, *Andreev*, 14 Aug 1909 (US).

5. *Cystopteris pellucida* (Franch) Ching

SPECIMENS EXAMINED:

CHINA.—MOUPIN.—(Thibet oriental), *David*, 1870 (P). YUNNAN.—*Delavay*, n.d. (P); in ravines, *Ducloux* 169 (P).

6a. *Cystopteris sudetica* A. Br. et Milde var. *sudetica*

SELECTED SPECIMENS:

CZECHOSLOVAKIA.—MORAVIA.—Ostsudeten-Altvatergebirge, Freiwalden, *Laus*, Aug 1935 (S-PA); near Holesov, *Gogela*, n.d. (S-PA).

HUNGARY.—Szepes, Hohen-Tatra, *Nyarady*, 5 Sep 1911 (S-PA); Piennineupass (Karpathen), *Ullepitsch*, Jul 1890 (S-PA); Maramaros, Borsabanya, *Boros*, 17 Jul 1942 (S-PA); Gomor, in valle Stracenensi, *Richter*, 11 Jul 1901 (S-PA, US).

NORWAY.—GUDBRANDSDALEN.—Nordra Fron, *Samuelsson & Zander*, 22 Jul 1934 (US); Kongsli, *Wall*, 22 Jul 1934 (S-PA).

POLAND.—Carpathians, Korvielisko, *Sagorski*, Jul 1887 (S-PA); Silesia, Jesenik (Gesenke) near Reiwiesen, *Laus*, Sep 1915 (S-PA); Allemagne, Silesie, Sudetes, *Laus*, Jul 1935 (S-PA).

ROMANIA.—Transilvania, Bihor district, *Pop*, 29 Aug 1935 (S-PA, US); Bucovina, near Pojana-Stampi (Eastern Carpathians), *Dorfler*, 1855 (L).

UNION OF SOVIET SOCIALIST REPUBLICS.—Tomsk, Kuznezow 675 (S-PA); Wolagda, *Zickendrath*, 18 Jul 1893 (S-PA).

6b. *Cystopteris sudetica* var. *moupinensis* (Franch.) Blasdell

SPECIMENS EXAMINED:

CHINA.—KANSU.—Sin-long-chan et Ma-ho-chan, *Licent* 4288 (P). MOUPIN.—*David*, 1870 (P). SHENSI.—Tai-pei-shan, *Purdom* 63 (S-PA, US). SIKANG.—between Taining (Ngata) and Taofu (Dawo), *Smith* 12098 (S-PA). SZECHUAN.—Karlong, *Smith* 4227 (S-PA); Dongrergo, *Smith* 3628 (S-PA).

7. *Cystopteris bulbifera* (L.) Bernh.

SELECTED SPECIMENS:

CANADA.—NEW BRUNSWICK.—Fairville, *Fowler*, 26 Jul 1877 (US). NEWFOUNDLAND.—Boone Bay, Shag Cliff, *Fernald et al.* 1121 (PH); Middle Arm, Bay of Islands, *Fernald et al.* 1120 (PH); Lower Humber Valley, between Marble Mountain and Humbermonth, *Fernald et al.* 1119 (PH); Highlands of St. John, W face of Bard Harbor Hill, *Fernald & Long* 27206 (PH). NOVA SCOTIA.—Gypsum area, Brooklyn, *McLellan*, 18 Jun 1938 (US); Victoria Co.: Port Bevis, *Fernald & Long* 19473 (PH). ONTARIO.—Bruce Peninsula, Umbrella Lake, *Krotkov* 9582 (US); Niagara Falls Glen, *Fisher*, 6 Aug 1901 (PH); Toronto, Don Valley, *Armstrong*, 25 Jul 1891 (US); Algoma District, Batchawana Falls, *Taylor et al.* 165 (US). Brant Co.: 2 mi. E of Ayr, *Soper and Dale* 4121 (US). Carleton Co.: Ottawa District, NW of Stanley Corners, *Senn et al.* 181 (TENN). Durham Co.: 7.5 mi. S of Lindsay, *Soper & Dale* 3867 (US). Grey Co.: 3 mi. NW of Owen Sound, *Wherry*, 20 Jun 1934 (PH). Leeds Co.: Kitley Twp., *Senn* 1665 (US). Peterborough Co.: ½ mi. NW of Westwood, *Wherry*, 5 Sep 1932 (PH). QUEBEC.—Beauce Co.: 3 mi. N of Leeds Station, *Wherry*, 24 Aug 1935 (PH). Gaspe Co.: W of Perce, *Henry* 1753 (PH). Barnston, near Stanstead, *Lucien & Sylvestre* 1540 (US); Georgeville, *Churchill*, 13 Aug 1886 (US); La Trappe, *Louis-Marie*, 1 Sep 1931 (PH); L'Ile d'Anticosti, *Marie-Victorin & Rolland-Germain* 24620 (PH, US); Oka, *Adrien* 1273 (PH).

UNITED STATES.—ALABAMA.—Colbert Co.: near Sheffield, *Mohr*, 8 Jun 1892 (US). Dade Co.: 9 mi. W of Trenton, *Howell*, 23 Jun 1913 (US). Madison Co.: in the vicinity of Huntsville, *Pollard & Maxon* 390 (US). Marshall Co.: Guntersville, *Howell* 817 (US). St. Clair Co.: St. Clair Spring near Ashville, *Mohr*, Jul 1880 (US). ARKANSAS.—Benton Co.: near Garfield, *Palmer* 44466 (US). Marion Co.: Bull Shoals Dam Reservoir, *Demaree* 29280 (PH). ARIZONA.—Coconino Co.: Oak Creek, 18 mi. SW of Flagstaff, *Goldman* 2188 (US). CONNECTICUT.—Canaan Mt., *Leggett*, Jul 1865 (PH). New Haven Co.: New Haven, *Safford* 397 (US). GEORGIA.—Floyd Co.: 3 mi. SW of Rome, *Duncan & Hardin* 15246 (US). ILLI

NOIS.—Cook Co.: Lemont, *Hill* 1152 (PH). Jo Daviess Co.: ¼ mi. S of Council Hill, *Lansing* 4146 (PH). Tazewell Co.: 5 mi. N of East Peoria, *Chase* 12739 (US). Will Co.: Lockport, *Skeels* 621 (US). INDIANA.—Crawford Co.: 6 mi. S of Leavenworth, *Tryon* 4434 (TENN, US). Harrison Co.: 3 mi. E of Elisabeth, *Deam* 20554 (US). Huntington Co.: ¼ mi. E of Andrews Stop along Wabash Valley Traction line, *Deam*, 7 Jul 1907 (PH). Lawrence Co.: Spring Mill State Park, *Cain* 6387 (TENN). Montgomery Co.: Pine Hills, *Friesner* 9711 (TENN). Putnam Co.: 3 mi. W of Groveland, *Friesner* 7086 (TENN). IOWA.—Clayton Co.: 8 mi. S of Guttenburg, *Wherry*, 1 Jun 1937 (PH). Clinton Co.: Clinton, *Pammel* 238 (US). Dubuque Co.: 2½ mi. NW of Durango, *Wherry*, 1 Jun 1937 (PH). Fayette Co.: Shaded lime-rocks, *Fink* 446 (US). Poweshiek Co.: Grinnell, *Jones* 1876 (PH). KENTUCKY.—Carter Co.: near Cascade Caverns, *Smith et al.* 3451 (US). Edmonson Co.: Mammoth Cave National Park, *Lix* 54 (US). Fayette Co.: Lexington, *Short*, n. d. (PH). Pulaski Co.: near Cedar Grove, *Wherry & Pennell* 13783 (PH). Warren Co.: Bowling Green, cave entrances, *Price*, Jun 1893 (PH). MAINE.—Aroostook Co.: McKiels Br., Allaguash River, *Fellows* 112 (PH). Franklin Co.: woods near Farmington, *Chamberlain & Knowlton*, 2 Sep 1904 (US). Penobscot Co.: Cedar swamp, Lee, *Steinmetz* 259 (US). Somerset Co.: woods on slopes of Green Mountain, *St. John & Nichols* 2068 (US). MARYLAND.—Washington Co.: Antietam, *Freeman*, 2 Aug 1936 (US). MASSACHUSETTS.—Berkshire Co.: vicinity of Tyringham, *Vail*, 18 Jul 1897 (PH). Franklin Co.: Roaring Brook, Leverett, *Adams*, 15 Aug 1870 (PH). Hampshire Co.: Shady woods, Amherst, *Clark*, Jul 1881 (PH). MICHIGAN.—Alger Co.: 8 mi. S of AuTrain, *Wherry & Leeds* 3377 (PH). Berrien Co.: 4 mi. N of Buchanan, *Wherry*, 9 Sep 1944 (PH). Cheboygan Co.: Cheboygan, *Kofoid*, 20 Aug 1890 (TENN). Crawford Co.: vicinity of Grayling, *Piper*, Jul 1922 (US). Eaton Co.: near Grand Ledge Clay Company quarry, *Wagner* 8078 (MICH). Grand Traverse Co.: along Boardman River NE of Kingsley, *Hagenah* 1342 (US). Ionia Co.: 4 mi. W of Lyons, *Wagner* 8080 (MICH). Kalkaska Co.: 2 mi. S. of Kalkaska on US-131, *Hagenah* 1313 (US). Kent Co.: S of Carlisle, *Wherry*, 25 June 1933 (PH, US). Mackinac Co.: Mackinac Island, *Hicks*, 30 Jun 1889 (US). Oakland Co.: Farmington, *Farwell* 6064 (US). Ontonagon Co.: Porcupine Mts., *Wherry & Leeds* 3341 (PH). St. Clair Co.: near Port Huron, *Dodge*, 26 Jul 1896 (TENN, US). MINNESOTA.—Clearwater Co.: Boholl Trail, *Grant* 3343 (US). Winona Co.: Winona, *Holzinger*, 10 Aug 1888 (US). MISSOURI.—Benton Co.: Limestone bluffs of Osage River, *Palmer* 35968 (US). Callaway Co.: Fulton, *Greger*, Jul 1896 (US). Laclede Co.: along Gasconade River, N of Hazel Green, *Steyermark* 8076 (US). Marion Co.: Hannibal, *Davis*, 6 Jul 1909 (PH). Phelps Co.: "Slaughter Sink" near Arlington, *Palmer & Steyermark* 41394 (PH, US). Ralls Co.: 2 mi. N of New London, *Wherry*, 8 Jul 1935 (PH). Shelby Co.: limestone creek bluffs, near Bethel, *Palmer & Steyermark* 40899 (PH). Stoddard Co.: Crowley's Ridge, near Painton, *Palmer* 34903 (PH). Washington Co.: near Bliss, *Steyermark* 7031 (US). NEW HAMPSHIRE.—Cheshire Co.: Keene, *Milligan*, Jul 1884 (US). NEW JERSEY.—Bergen Co.: Closter, *Austin*, n.d. (US). Sussex Co.: E of Newton, *Dowell* 5024 (US). Warren Co.: Cedar Lake, SW of Blairstown, *Smith*, 25 Aug 1895 (PH). NEW MEXICO.—Canyon above Grey's Ranch, Guadelupe Mts., *Goodding*, 29 Aug 1937 (US). NEW YORK.—Broome Co.: Day's Glen, vicinity of Lisle, *Dowell* 4140 (US). Clinton Co.: Valcour Island, *Baim & Smith* 2963 (US). Dutchess Co.: vicinity of Clove, *Standley & Bollman* 11880 (US). Essex Co.: Ansable Chasm, *Leeds* 55 (PH). Greene Co.: ravine SE from Haines Falls, *Wherry*, 25 Jun 1946 (PH). Herkimer Co.: Old Forge, Limekiln Creek, *Dowell* 4477 (US). Madison Co.: vicinity of Oneida, *Maxon*, 24 Jun 1895 (US). Monroe Co.: Telephone Road, East Henrietta, *Matthews* 4392 (PH). Niagara Co.: Niagara Falls, *Shurtleff*, n.d. (US). Onondaga Co.: near Syracuse, *Myers*, n.d. (US). Schenectady Co.: *Fisher*, Oct 1896 (PH). Schoharie Co.: Sharon Springs, *House* 19547 (US). Schuyler Co.: Watkins Glen, *Rau*, 8 Sep 1871 (PH). Tompkins Co.: Six Mile Creek, Ithaca, *Eames & MacDaniels* 3382 (US). Ulster Co.: vicinity of Shandaken, *Miller*, 16 Aug 1901 (US). Washington Co.: 1 mi. E of Argyle, *Schaeffer*

2191 (PH). Wyoming Co.: Wyoming, *Hartnell*, 13 Jun 1903 (PH). Yates Co.: Penn Yan, *Hartnell*, n.d. (PH). NORTH CAROLINA.—Madison Co.: 4 mi. W of Hot Springs, *Oosting* 35305 (PH, US). Swain Co.: Blowing Springs, Nathahale Gorge, *Blomquist & Anderson* 1653 (PH). OHIO.—Clark Co.: 5 mi. W of Springfield, *Leeds* 3189 (PH). Erie Co.: Swifts' Hollow, Vermilion River, *Grover*, 13 Jul 1900 (US). Geauga Co.: Thompson, *Werner*, 27 Sep 1885 (US). Hamilton Co.: *Mohr*, n.d. (US). Loraine Co.: Elyria, *Steele*, Jul 1874 (US). Ross Co.: Point Creek, *Brown*, 23 May 1953 (MICH). Sandusky Co.: vicinity of Freemont City, *Leonard* 2118 (US). PENNSYLVANIA.—Allegheny Co.: Moon Twp., *Hatry*, 18 May 1902 (PH, US). Beaver Co.: Crows Run, *Shafer*, 31 Jul 1885 (PH). Blair Co.: Limestone cliffs at Arch Spring, *Canan*, 1941 (PH). Bradford Co.: Troy, *Bartram*, 19-20 Jul 1913 (PH). Center Co.: 1½ mi. S. of Bellefonte, *Leeds* 3567 (PH). Clinton Co.: 3 mi. SW of Hyner, *Wherry*, 1 Jun 1941 (PH). Columbia Co.: ½ mi. SW of Catawissa, *Wherry*, 29 Jul 1938 (PH). Dauphin Co.: entrance to Indian Echo Cave, S of Hummelstown, *Wherry*, 30 Jun 1934 (PH). Fayette Co.: Ohiopyle, *Brown et al.* 132 (PH). Franklin Co.: Mercersburg, *Porter*, 27 Oct 1845 (PH). Greene Co.: near Crabapple, *Myers*, 7 Jul 1935 (PH). Huntingdon Co.: near Alexandria, *Porter*, Jul 1845 (PH). Laikar Co.: *Turning*, Aug 1906 (PH). Lancaster Co.: near Lancaster, *Small*, 15 Jul 1890 (US). Lawrence Co.: above Rock Point, *Jennings*, 26 Jul 1909 (PH). Mifflin Co.: ½ mi. S of Honey Creek, *Wherry*, 13 Aug 1942 (PH). Monroe Co.: stream at Rosscommon, *Rau*, 21 Jul 1878 (PH). Northampton Co.: 1 mi. E of Kreidersville, *Schaeffer* 13930 (US). Pike Co.: Bushkill Falls, *Brown*, 30 May 1897 (PH). Susquehanna Co.: near Ararat, *Saunders*, 8-20 Jul 1900 (PH). Tioga Co.: 2 mi. NW of Kennedy, *Leeds* 580 (PH). Union Co.: 1 mi. W of White Deer, *Wherry*, 16 Apr 1938 (PH). Wayne Co.: 2 mi. N of L. Shehauken, *Dix*, Jul 1936 (PH). Wyoming Co.: ½ mi. SE of Tunkhannock, *Pretz* 7255 (PH). York Co.: near Philadelphia, *Crawford*, 2 Jul 1904 (PH). TENNESSEE.—Anderson Co.: E of Clinch River, *Shaver* 10302 (TENN). Bledsoe Co.: below Low Gap, *Shanks et al.* 4474 (TENN). Bedford Co.: near Normandy, *Shaver* 10457 (TENN). Blount Co.: NE end of Jones Bend, *Shaver* 10639 (TENN). Bradley Co.: 3.3 mi. E of Charleston, *Shaver* 10146 (TENN). Campbell Co.: Cedar Creek, *Sharp et al.* 3353 (TENN). Cannon Co.: 7 mi. NE of Woodbury, *Shaver* 10219 (TENN). Cheatham Co.: Craggie Hope, *Svenson* 4208 (PH). Claiborne Co.: west side of Clinch River, *Shaver* 10469 (TENN). Clay Co.: W of Cumberland River and Celina, *Shaver* 10552 (TENN). Cocke Co.: N of Newport, *Shaver* 10395 (TENN). Coffee Co.: near Tullahoma, *Sharp et al.* 4748 (TENN). Cumberland Co.: Ozone Falls, *Shanks et al.* 13823 (TENN). Fentress Co.: 8 mi. N of Jamestown, *Shaver* 10262 (TENN). Grainger Co.: Tampico, *Morrison & Brown* 82 (TENN). Greene Co.: near Chaney, *Shaver* 10693 (TENN). Hamblen Co.: 4 mi. N of Morristown, *Wherry*, 24 Aug 1937 (PH). Hamilton Co.: N of Red Bank, *Shaver* 10630 (TENN). Hawkins Co.: Chestnut Ridge, *Wolfe* 489 (TENN). Humphreys Co.: 6 mi. N of Waverly, *Shaver* 10538 (TENN). Jefferson Co.: north-facing bluffs down the Holston River, *Shaver* 10684 (TENN). Johnson Co.: 8 mi. N of Mountain City, *Shaver* 10381 (TENN). Knox Co.: Baker's Bluff, *Rice* 411 (TENN). Lawrence Co.: W of Lawrenceburg, *Wherry*, 22 Aug 1937 (PH). Loudon Co.: near Hickory Creek, *Shaver* 10499 (TENN). Marion Co.: Battle Creek, *Sharp & Underwood* 2520 (TENN). Meigs Co.: NW of Decatur, *Shaver* 10606 (TENN). Montgomery Co.: W of Ringgold, *Shanks* 970 (TENN). Rhea Co.: near the Tennessee River, *Shaver* 10590 (TENN). Roane Co.: Harriman Bluffs, *Sharp & Underwood* 2053 (TENN). Robertson Co.: road from Joelton to Greenbrier, *Shaver* 4307 (TENN). Rutherford Co.: Snail Shell Cave, *DeSelm* 977 (D, TENN). Sevier Co.: Cherokee Orchard, *Rice* 411 (TENN). Smith Co.: 1.8 mi. N of Chestnut Mound, *Shaver* 10138 (TENN). Union Co.: .9 mi. N of the Knox Co. line, *Shaver* 10669 (TENN). Van Buren Co.: E of Spencer, *Shaver* 10576 (TENN). Washington Co.: NW of Philadelphia, *Shaver* 10653 (TENN). Wayne Co.: SE of Waynesboro, *Sharp et al.* 9612 (TENN). White Co.: W of Sparta, *Shanks et al.* 5013 (TENN.) UTAH.—Elk Mountains, *Rydberg & Garrett* 9343 (US). VERMONT.—Bennington Co.: Dorset, *Terry*, 29 Aug 1905 (US). Caledonia Co.:

Barnet, *Stevens*, 14 Jul 1892 (US). Chittenden Co.: Richmond, *Doray*, 28 Jun 1944 (US). Cumberland Co.: Pownal, *Knowlton*, 14 Jun 1918 (PH). Lamoille Co.: Eden, *Knowlton*, 20 Jul 1916 (PH). Orleans Co.: Willoughby, *Knowlton*, 24 Aug 1918 (PH). Rutland Co.: Burlington, *Jones & Eggleston*, 4 Aug 1893 (US). Windsor Co.: Woodstock, *Kittredge*, 13 Aug 1920 (PH). WEST VIRGINIA.—Fayette Co.: Quinnemont, *Pollard & Maxon* 10 (US). Greenbrier Co.: SW of Renick P. O., *Wherry*, 10 Jul 1938 (PH). Jefferson Co.: Harper's Ferry, *Henshaw*, 4 Jul 1884 (US). Mercer Co.: NE of Bluefield, *Wherry*, 18 July 1938 (PH). Monroe Co.: near Greenville, *Morris* 1026 (US). Pendleton Co.: Mouth of Seneca, *Leeds* 264 (PH). Randolph Co.: SE of Huttonsville, *Wherry*, 7 Jul 1938 (PH). VIRGINIA.—Alleghany Co.: NE of Covington, *Wherry*, 27 Aug 1938 (PH). Bath Co.: Jackson River Gorge, *Henry* 2181 (PH). Craig Co.: Potts Creek Valley, *Steele* 174 (US). Fairfax Co.: Potomac Bluff, Langley, *Palmer*, 13 Jul 1902 (PH). Frederick Co.: Shenandoah, *Cresson* 108 (PH). Giles Co.: Harveys Cave Sinkhole, *Iltis* 1882 (TENN). Highland Co.: N of Franklin, *Leeds* 263 (PH). Lee Co.: E of Pennington Gap, *Leeds* 176 (PH). Montgomery Co.: 2 mi. E of East Radford, *Adams & Wherry* 2259 (PH). Patrick Co.: north approach to Pinnacles of Dan, *Wherry*, 5 Sep 1946 (PH). Rock Bridge Co.: Natural Bridge, *Sowden*, 9 Jun 1923 (PH). Russell Co.: W of Dickensonville, *Leeds* 477 (PH). Smyth Co.: near Marion, *Small*, 22 May 1892 (PH, US). Washington Co.: 2 mi. NE of Bristol, *Wherry*, 8 Jun 1934 (PH). Wythe Co.: S of Eagle, *Wherry*, 14 Jul 1936 (PH). WISCONSIN.—Brown Co.: DePere, *Kellogg*, 4 Jul 1888 (US). Door Co.: Ephraim, *Millspaugh* 3954 (US). Polk Co.: at Osceola, *Tryon & Tryon* 4339 (TENN, US). Sauk Co.: near Merrimac, *Wherry & Leeds* 3306 (PH). Trempealeau Co.: Trempealeau, *Fassett* 4098 (PH).

8. *Cystopteris diaphana* (Bory) Blasdell

SELECTED SPECIMENS:

NORTH AMERICA

COSTA RICA.—Coliblanco, *Maxon* 312 (US); Cartago, Cartago, *Cooper*, Apr 1888 (US); San Jose, Las Nubes, *Standley* 38357 (US); Region of Zarcero, *Smith*, n.d. (US).

GUATEMALA.—Chimaltenango, Santa Elena, *Skutch* 290 (US). Chiquimula, Volcan Ipala, *Steyermark* 30559 (US). Guatemala, *Smith* 2424 (US). San Marcos, Volcan Tajumulco, *Steyermark* 36783 (US).

HAITI.—Petionville, *Ekman* 1436 (US).

JAMAICA.—trail from St. Helens Gap to Latimer River, *Maxon & Killip* 901 (US); summit of Blue Mountain Peak, *Maxon* 1400 (US).

MEXICO.—Chiapas, San Cristobal, *Münch* 60 (US). Chichuahua, Sierre Madre, *Nelson* 6146 (US). Distrito-Federal, Guajimalpa, *Matuda* 20994 (US). Durango, Metates, N of Cueva, *Pennell* 18437 (PH). Jalisco, above Jazmin, *McVaugh* 10065 (US). Mexico, Popo Park, *Hitchcock*, 4-8 Aug 1910 (US). Michoacan, vicinity of Morelia, *Arsene* 6899 (US). Morelos, El Parque, *Oreutt* 3845 (US). Nayarat, territory of Tepic, *Rose* 2207 (US). Oaxaca, Sierra de San Felipe, *Smith* 2065 (US). Puebla, Hueyotlipan, *Arsene*, 15 Jun 1908 (US). Vera Cruz, Orizaba, *Copeland* 35a (US).

PANAMA.—vicinity of El Boquete, Chiriqui, *Maxon* 5238 (US). Quebrada Velo Volcano, *Woodson & Schery* 245 (US).

SOUTH AMERICA

ARGENTINA.—Catamarca, Belen, *Sleumer & Vervoorst* 2462 (US). Cordoba, Sierra Chica, *Osten*, 9 May 1917 (S-PA). Tucuman, Burroyaco, *Venturi* 8026 (S-PA).

BOLIVIA.—Undnavi, Nordyungas, *Buchtien* 2671 (S-PA). Larecaja, Sorata, *Mandon*, Jul 1857 (S-PA). La Paz, Incaihaca, *Asplund* 3746 (US). Near Pelichuco, *Williams* 2615 (US).

BRAZIL.—Santa Catarina, Riozinho, *Smith & Klein* 7889 (US). Rio Grande do Sul, Sao Leopoldo, *Dutra* 213 (R).

CHILE.—Santiago, San Cristobel, *Hastings* 105 (US).

COLUMBIA.—Caldas, Paramo del Quindio, *Pennell & Hazen* 12118 (US). Cundinamarca, 18 km. E of Cabrera, *Fosberg* 20764 (US). El Cauca, Coconuco, *Killip* 6845 (US). Narino, W of Ipiales, *Ewan* 16106 (US).

ECUADOR.—Azuay, E of Cuenca, *Correll* E355 (US). Bolivar, on road from Guaranda to Ambato, *Correll* E441 (US). Cotopaxi, *Haught* 2930 (US). Imbabura, Mariano Acosta, *Wiggins* 10287 (US). Pichincha, near Quito, *Sydow*, 30 Sep 1937 (S-PA, US). Tungurahua, 15 km. above Ambato, *Correll* E307 (US).

PERU.—Lucumayo Valley, *Cook & Gilbert*, 19 Jun 1915 (US). Calca, Cuzco, Vilcabamba, *Vargas* 4004*a* (US). Ollantaytambo, *Cook & Gilbert* 742 (US). Rio Blanco, *Macbride & Featherstone* 703 (US).

VENEZUELA.—Sucre, Cerro Turumuquire, *Steyermark* 62552 (US). Merida, S. Rafael de Mucuchies, *Pittier* 12914 (US). Merida, Mucuruba, *Gehriger* 303 (US).

AFRICA AND EUROPE

ABYSSINIA.—*Schimper*, n.d. (L).

BELGIAN CONGO.—Kivu, Volcan Mikeno, *Humbert* 8006 (US).

CANARY ISLANDS.—Gran Canaria, San Mateo, *Asplund* 85 (S-PA). La Palma, *Bornmüller*, 24 Apr 1901 (S-PA). Tenerife, Beo del Rio, *Pitard*, Feb 1906 (L, S-PA). Tenerife, La Perdoma la madre del agua, *Burchard* 30 (S-PA).

MADEIRA ISLAND.—Funchal, *Sederholm*, 30 Dec 1884 (S-PA).

NATAL.—*Wood*, n.d. (S-PA).

PORTUGAL.—Lusitania, Estremadura, near Capuchos, *Rainha* 8849 (US).

TANGANYIKA TERRITORY.—Kilimandjaro, *Daubenberger*, Apr 1906 (L, S-PA).

9. *Cystopteris japonica* Lssn.

SELECTED SPECIMENS:

CHINA.—Kouy-Tcheow, *Cavalerie*, 4 Sep 1902 (L, S-PA). Szechuan, Ta-hsiangling, *Smith* 2124 (S-PA).

JAPAN.—Honshu.: Nara, N of Zenkiguti, *Tagawa* 5842 (US); Musashi, Nagurimura, *Hamegata* 2904 (US); Hyogo, Koranotaki, Satiyomura, *Tagawa* 6485 (US); Shikoku.: Mt. Yologura, Takaokagun, Kochi-ken, *Uno* 2611 (US). Nanokawa, Tosa, Sikok, *Watanabe*, 11 Jul 1892 (P).

10. *Cystopteris tenuisecta* (Bl.) Mett.

SELECTED SPECIMENS:

BORNEO.—Mt. Kinabalu, *Clemens*, 28 Jun 1933 (L).

CEYLON.—*Parish*, 1868 (P).

CHINA.—Yunnan.: Mengtze, *Hancock*, 1893-5 (US); Shweli River drainage basin, E of Tengyueh, *Rock* 7722 (US).

INDIA.—Assam, Cherrapunji, Khasi Hills, *Mann*, Sep 1888 (L). Sikkim, *Thomson*, n.d. (US). Manipur, *Buysman* 2908 (P).

JAPAN.—mountains of Yoshino, *Faurie* 220, Sep. 1913 (S-PA).

INDOCHINA.—Tonkin, *Petelot*, Jul 1920 (P).

JAVA.—Mt. Gede, Kandang badak, *Danser*, 17 Dec 1925 (L).

MALAYA.—Pahang, Cameron Highlands, *Holttum*, 10 May 1936 (US).

PHILIPPINE ISLANDS.—Luzon, Pauri, *Merrill* 8381 (L).

SUMATRA.—Gojor, *Van Daalen*, 1904 (L).

TAIWAN.—Arisan, *Faurie* 661 (S-PA). Bunkikiyo, *Faurie* 387 (S-PA).

HYBRIDS

1. *Cystopteris* × *tennesseensis* Shaver

SELECTED SPECIMENS:

ARKANSAS.—Benton Co.: Martins Bluff, *McGregor* 3722 (US). Randolph Co.: Revenden Springs, *Demaree* 29202 (PH). KANSAS.—Bourbon Co.: 2 mi. S of Uniontown, *McGregor* 1778 (US). Chautauqua Co.: near Sedan, *Palmer* 41805 (US). Montgomery Co.: 8 mi. W of Sycamore, *McGregor* 2399 (US). Wilson Co.: 2 mi. W of Neodesha, *McGregor* 3404 (US). KENTUCKY.—Edmonson Co.: Mammoth Cave National Park, *Lix* 29 (US). Hardin Co.: Vertres, *Wherry & Pennell* 13632 (PH). Powell Co.: Natural Bridge, *McCoy*, 23 Jun 1934 (PH). MISSOURI.—Greene Co.: vicinity of Willard, *Standley* 9650 (US). McDonald Co.: 3 mi. NE of Noel, *McGregor* 3641 (US). Morgan Co.: N of Florence, *Wherry*, 26 May 1940 (PH). Pike Co.: 11 mi. NNW of Bowling Green, *Wherry*, 8 Jul 1935 (PH). NORTH CAROLINA.—Craven Co.: E of Fort Barnwell, *Radford* 5618 (US). OKLAHOMA.—Delaware Co.: *McGregor* 3749 (US). Pontotoc Co.: 4 mi. SE of Ada, *Waterfall* 8385 (PH). TENNESSEE.—Dekalb Co.: between Dowelltown and Smithville, *Shaver* 10505 (TENN, US). Giles Co.: near Waco, *Shaver* 10220 (TENN, US). Grundy Co.: road to Beersheba Springs, *Shaver* 10188 (TENN). Hardin Co.: east of Olive Hill, *Shaver* 10533 (TENN). Hickman Co.: Centerville, *Shaver* 10526 (TENN, US). Lewis Co.: 4 mi. N of Hohenwald, *Shaver* 10222 (TENN). Lincoln Co.: 10 mi. S of Fayetteville, *Shaver* 10280 (TENN). Macon Co.: 6 mi. E of Lafayette, *Shaver* 10555 (TENN). Marshall Co.: road from Cornersville toward Diana, *Shaver* 10460 (TENN). Overton Co.: 3 mi. SE of Livingston, *Shaver* 10550 (TENN). Perry Co.: 11 mi. W of Lewis Co. line, *Shaver* 10215 (TENN). Smith Co.: Rome, *Shaver* 10427 (Type locality, TENN, US). Trousdale Co.: 4 mi. NE of Hartsville, *Shaver* 10485 (US). Wayne Co.: Forty-nine Creek, *Shaver* 10531 (TENN). TEXAS.—Culberson Co.: Guadalupe Mts., Devils Canyon, *Moore & Steyermark* 3561 (US).

2. *Cystopteris* × *laurentiana* (Weath.) Blasdell

SELECTED SPECIMENS:

CANADA.—NEWFOUNDLAND.—Port au Port, *Kennedy* 90 (GH); Mt. Moriah, *Fernald et al.* 26152 (PH, US); W. Arm, Bonne Bay, *Fernald et al.* 1123 (PH); Highlands of St. John, *Fernald et al.* 27214 (PH). NOVA SCOTIA.—Cape Breton Island, *Nichols* 678 (GH). ONTARIO.—Manitoulin Island, *Pease & Ogden* 24,997 (US); 15 mi. E of Port Arthur, *Tryon & Faber* 4919 (US). Bruce Peninsula, Dyer Bay, *Pease & Ogden* 24,871 (US); Brinkman's Corners, *Taylor* 6129 (US). Thunder Bay District, at International Bridge, *Carton* 1859 (US). QUEBEC.—Gaspe Co.: Cap Pleureuse, *Fernald & Weatherby* 2402 (US); Cap-Rosier, *Marie-Victorin* 17040 (GH, US); Petite Tourelle, *Marie-Victorin et al.* 3897 (US). Beauce Co.: 3 mi. N of Leeds Station, *Wherry*, 24 Aug 1935 (PH). Rimouski Co.: Bic, *Bartram & Long* 259 (PH); headland north of Baptiste Michaud's, Bic, *Collins & Fernald*, 18 Jul 1904 (TYPE, GH). Iles de la Madelein.: Cap-aux-Meules, *Marie-Victorin* 9333 (GH). Ile Nue, *Marie-Victorin & Rolland-Germain* 24618 (GH). Matane Co.: near base of Mt. Nicolabert, Joffre, *Fernald & Pease* 24790 (GH).

UNITED STATES.—MINNESOTA.—Lake Co.: Manitou Falls, *Tryon et al.* 4894 (US). PENNSYLVANIA.—Centre Co.: 3 mi. NNE of Pennsylvania State College, *Wahl* 1449 (PH). Pike Co.: Kimbles Station, *Wherry*, 24 Jun 1936 (PH).

3. *Cystopteris* × *alpina* (Wulfen) Desv.

SELECTED SPECIMENS:

ALBANIA.—"Prokletija," *Dorfler*, 18 Jul 1914 (S-PA).

AUSTRIA.—S Tyrol, *Rosenstock*, Jul 1897 (L). Carinthia, *Suringar*, n.d. (L). Salzburg, *Sauter*, n.d. (L).

FRANCE.—Haute Savoie, Mt. Vergy, *Bourgeau*, 27 Jul 1873 (P). Savoy, *Suringar*, 1865 (L). Basses-Alpes, L'Arche, *no coll.* (S-PA).

GERMANY.—Bayern Partenkirchen, *Harz*, 10 Sep 1920 (S-PA). Bayern, Oberstdorf, *no coll.* Jul 1920 (S-PA). Sachsen, *no coll.* (S-PA).

GREECE.—Mt. Parnassos, *Orphanodes*, 30 Jul 1854 (S-PA). Peloponnesus, Achaia in mt. "Chelmos" (Aroania), *Bornmüller*, 19 Jun 1926.

HUNGARY.—Lika-Kibava Croatiae, *Filarszky & Kummerle*, 4 Jul 1911 (S-PA) Jatri, *Pawdbroch*, 15 Jul 1922 (S-PA).

ITALY.—Piedmont, Cottian Alps, *Roslan*, 1880 (S-PA). Lombardy, Val di Pona, *Levier*, Jul 1867 (S-PA). Dolomites Mts., Colfosco, *Werdermann & Meyer*, 5 Aug 1956 (US). Sicily, Mt. Aetna, *Huet du Pavillon*, 12 Jul 1855 (L).

JUGOSLAVIA.—Montenegro ad Cirova Pecina, Mt. Durmitov, *Muryev*, 27 Jun 1930 (S-PA).

SWITZERLAND.—Glarus, *Sinia*, 9 Aug 1927 (L). Vaud, *Masson*, 11 Jul 1876 (S-PA). Valais, *Wilczek*, 17 Jul 1905 (S-PA). Waadt, *Kuhlmann & Wirtgen*, n.d. (S-PA). Unterwalden, *Samuelsson*, 10 Jul 1921 (S-PA).

4. *Cystopteris diaphana* × *fragilis* complex

SELECTED SPECIMENS:

NORTH AMERICA

ALASKA.—Mt. McKinley National Park, *Nelson* 4100 (US); Skagway, *Eastwood* 749 (US). Cook Inlet, *Coville & Kearney* 2437 (US); Cape Nome, *Blaisdell*, 1900 (US); Kodiak Isl., Olga Bay, *Looff*, Aug 1938 (US). Aleutian Islands.: Sitka, Mt. Venstovoi, *Evermann* 233 (US); St. Paul Island, *Townsend*, Aug 1893 (US); Umnak Island, Nikolski, *Hulten* 7134 (US); Attu Island, Holtz Bay, *Schaack* 360 (US); Unalaska, *Turner & Rust*, 1879-81 (PH).

CANADA.—ALBERTA.—Waterton Lakes National Park, *Breitung* 16091 (US); Fort Chipewyan, *Raup* 6053 (US); Lake Louise, *Brown* 717 (PH). BRITISH COLUMBIA.—Vancouver Island, vicinity of Victoria, *Macoun* 545 (US); near Fish Lake, *Shaw* 1211 (US); Brackendale, Squamish River, *Macoun* 92740 (US). LABRADOR.—Battle Harbor, *Waghorne*, 30 Aug 1891 (US). NEW BRUNSWICK.—Gloucester Co., Caraquet, *Dore & Gorham* 45796 (US); Kent Co., cliffs of Bon Ami, *Fowler*, 25 Aug 1866 (PH). NEWFOUNDLAND.—region of Ingornachoix Bay, Gargamelle Cove, *Fernald et al.* 1122 (PH, US); Avalon Peninsula, Placentia, *Williamson* 364 (PH); Bay of Islands, *Eames & Godfrey* 5776 (PH); Straits of Belle Isle, Big Brook, *Pease & Griscom* 27209 (PH); Brig Bay, *Fernald et al.* 26151 (PH). ONTARIO.—Grey Co., Owen Sound, *McColl*, Sep 1919 (S-PA, US); Thunder Bay District, 11 mi. NE of Port Arthur, *Garton* 1320 (US); Durham Co., 8 mi. S of Lindsay, *Soper & Dale* 3873 (US); Sault Ste. Marie, *Hermann* 7264 (PH). QUEBEC.—Matane Co., Mt. Logan, *Fernald & Pease* 24784 (US); Gaspe Co., Bonaventure Island, off Perce, *Storer* 270 (US); Rimouski Co., Bic, *Churchill*, 15 Jul 1905 (PH); Labelle Co., Nominingue, *Heroux & Roy*, 15 Jul 1932 (PH); McGregor Lake, near Ottawa, *Malte*, 13 Jun 1923 (S-PA); James Bay, Charlton Island, *Porsild* 4277 (S-PA). YUKON.—Yukon River, 3 mi. above Fortymile River, *Collier* 23 (US).

COSTA RICA.—Irazu Volcano, *Lankester* 655 (US).

DOMINICAN REPUBLIC.—San Juan, Sabana Neuva, *Howard* 9112 (US).

GREENLAND.—Disco, Godhaven, *Porsild*, 10-20 Sep 1922 (US); Ymer Island, *Seidenfaden* 380 (S-PA); head of Söndre Strömfjord, *Erlanson* 2430 (US); Tugtup Agtakorfia, Julianehaab District, *Gordon*, Aug 1923 (PH); North Star Bay, University Ridge, *Ekblaw* 11 (S-PA).

GUATEMALA.—Dept. Alta Verapaz, Coban, *Tuerckheim* 8630 (US).

HAITI.—gorge of River Chota, *Ekman* 5986 (US).

ICELAND.—Laxardal, *Palsson* 4 (PH); Grenujadastad, *Taylor*, 4 Jul 1895 (US);

Hofsskard, *Davidsson*, 19 Aug 1897 (US); Skagafjordur, Keta, *Sorensen*, 1930 (US); Gullbringusysla, Kapellukraun, Lambhagi, *Love*, 11 Sep 1949 (S-PA).

JAMAICA.—near Castleton Botanical Garden, *Underwood* 456 (US); trail from Cinchona to Blue Mt. Peak, *Maxon* 1495 (US); summit of Blue Mountain Peak, *Maxon* 9903 (US).

MEXICO.—Vera Cruz, Mt. Orizaba, *Seaton* 162 (US); Distrito-Federal, Contreras, *Orcutt* 3477 (US); Durango, Metates, north of Cueva, *Pennell* 18404 (US); Hidalgo, S. Miguel Regla, *Lyonnet* 2011 (US); Michoacan, Zacapu, *Leeds* 232 (PH); Jalisco, near Atequizallan, *Correll* 14364 (PH).

UNITED STATES.—ARIZONA.—Apache Co.: Hannagan Meadows, *Phillips* 2812 (US). Cochise Co.: Chuicahua National Forest, *Eggleston* 10791 (US). Coconino Co.: Clover Springs, *Collom* 948 (US). Pima Co.: Happy Valley, *Phillips* 2864 (US). CALIFORNIA.—Butte Co.: Butte Creek Canyon, *Austin* 244 (US). Fresno Co.: Kings Canyon, *Storer* 182 (US). Mendocino Co.: Ukiah, *Bolander*, Apr 1860 (US). Modoc Co.: Emerson Peak, Warner Mts., *Alexander & Kellogg* 5059 (US). San Bernardino Co.: San Bernardino Mts., *Parish* 3126 (US). Siskiyou Co.: Paradise Lake, Marble Mts., *Alexander & Kellogg* 5865 (US). Sonoma Co.: at foot of Mt. Hood, *Heller*, 26 Jun 1902 (US). Tulare Co.: Bakeoven Meadows, *Howell* 27130 (US). COLORADO.—Clear Creek Co.: Idaho Springs, *Smith*, 20 Jul 1884 (PH). El Paso Co.: Colorado Springs, *Smith*, 6 Aug 1881 (PH). Mexa Co.: S of Fruita, *Pennell & Schaeffer* 22120 (PH). Montrose Co.: 35 mi. W of Montrose, *Wherry*, 20 Jul 1937 (PH). Routt Co.: NE of Steamboat Springs, *Wherry*, 15 Jun 1937 (PH). San Juan Co.: Red Mt. Pass, *Wherry*, 18 Jul 1937 (PH). San Miguel Co.: 2½ mi. SW of Sam Station, *Wherry*, 19 Jul 1937 (PH). CONNECTICUT.—London Co.: N. Stonington, *Jausson*, 5 Sep 1927 (S-PA). New Haven Co.: Oxford, *Harger* 3769 (PH). IDAHO.—Bear Lake Co.: Montpelier, *Pennell*, 17 Jun 1931 (PH). Blaine Co.: Poison Creek, Sawtooth National Forest, *Woods & Tidestrom* 2626 (US). Idaho Co.: Lochsa, *Rose* 414 (US). Nez Perces Co.: Lake Waha, *Heller* 3295 (US). Owyhee Co.: 10 mi. E of Silver City, *Davis* 2083 (PH). IOWA.—Cass Co.: near Lewis, *Fay* 5169 (US). Clayton Co.: S of McGregor, *Wherry*, 1 Jun 1937 (PH, US). Emmett Co.: SW of Esterville, *Wherry*, 2 Jun 1937 (PH). KANSAS.—Douglas Co.: Lawrence, *Stevens*, n.d. (US). MAINE.—Penobscot Co.: Bangor, *Chickering*, Jun 1859 (US). Somerset Co.: Carratunk Falls, *Collins*, 8 Jul 1885 (US). MASSACHUSETTS.—Berkshire Co.: Mt. Washington, *Meredith*, 31 Jul 1922 (PH). Hampshire Co.: Middlefield, *Fernald & Long* 8354 (PH). Worcester Co.: Princeton, Mt. Wachusett, *Collins*, 5 Jul 1893 (US). MICHIGAN.—Gratiot Co.: Alma, *Davis*, Jul 1889 (US). Houghton Co.: Silver Mountain, *Richards* 2318 (S-PA). Keweenaw Co.: gorge of Eagle River, *Richards* 2057 (S-PA). Polk Co.: St. Croix Falls, *Wherry & Leeds* 3311 (PH). Marquette Co.: E of Ishpeming, *Wherry & Leeds*, 4 Jul 1935 (PH). St. Joseph Co.: Klinger Lake, *Wherry*, 7 Jun 1948 (PH). Washtenaw Co.: Dixboro, *Hermann* 6902 (PH). MINNESOTA.—Carlton Co.: Midway Creek, *Cronquist* 3853 (S-PA). Cook Co.: S of Clearwater Lake, *Butters & Buell* 464 (US). Washington Co.: 1½ mi. N of Point Douglas, *Moore* 10012 (US). Winona Co.: Dakota, *Mellele*, Aug 1934 (S-PA) MISSOURI.—Barry Co.: road between Cassville and Galena, *Wilkens* 2529 (PH). MONTANA.—Glacier Co.: Glacier National Park, Logan Pass, *Benner* 5074 (PH). NEVADA.—Clark Co.: Charleston Mts., Little Falls, *Clokey* 5373 (US). Elko Co.: Fox Creek Fork, *Train* 786 (PH). Leander Co.: Bunker Hill, *Kennedy* 4179 (PH). Mineral Co.: Cat Creek, *Alexander & Kellogg* 4474 (US). NEW JERSEY.—Essex Co.: Orange Mts., Newark, *Lyon*, 11 Aug 1896 (US). NEW MEXICO.—Dona Ana Co.: Organ Mts., *Wooton*, 16 Aug 1895 (US). Lincoln Co.: Ruidoss Creek, *Wooton*, 10 Jul 1895 (US). Otero Co.: Cloudcroft, *Viereck*, 29 May 1902 (PH). Rio Arriba Co.: Chama, *Standley* 6628 (US). San Miguel Co.: Pecos, *Bartlett*, Sep 1904 (US). Santa Fe Co.: 7 mi E of Santa Fe, *Heller*, 7 Jul 1897 (US). Socorro Co.: Mogollon Mts., *Wooton*, 8 Aug 1900 (US). Union Co.: Sierra Grande, *Standley* 6167 (US). NEW YORK.: Allegany Co.: Alma Hill, *Clausen*, 18 Jun 1939 (US). Tompkins Co.: Six Mile Creek, Ithaca, *Metcalf* 7385 (US). Washington Co.: Kingsbury, *Burnham*, 13

Aug 1916 (S-PA). NORTH CAROLINA.—Avery Co.: *Wherry*, 24 Aug 1938 (PH). Mitchell Co.: Roan Mt., *Smith*, 13 Jul 1880 (US). Watauga Co.: Grandfather Mt., *Leeds* 58 (PH). NORTH DAKOTA.—Morton Co.: Mandan, *Sarvis* 53 (US). OREGON.—Clackamas Co.: Oregon City, *Foster*, 20 Jun 1906 (PH). Douglas Co.: Nichols Station, *Ward* 31 (US). Klamath Co.: near Keno, *Applegate* 2010 (US). Lake Co.: Big Lake, *Eggleston* 7003 (US). Multonomah Co.: vicinity of Portland, *Palmer* 1493 (US). Union Co.: 15 mi. NW of Elgin, *Wherry*, 2 Jul 1931 (PH). PENNSYLVANIA.—Blair Co.: Hollidaysburg, *Wherry*, 20 Sep 1941 (PH). Bradford Co.: 5 mi. NW of Towanda, *Wherry*, 13 Aug 1935 (PH). Cameron Co.: Sterling Run, *Wherry*, 5 Sep 1940 (PH). Lycoming Co.: Clarketown, *Wherry*, 2 Jun 1941 (PH). Mercer Co.: Leesburg, *Wherry*, 30 Aug 1939 (PH). Montgomery, Conshohocken, *Banes*, 6 Aug 1891 (S-PA). Pike Co.: Kimbles, *Wherry*, 24 Jun 1936 (PH). Somerset Co.: Petersburg, *Brown & Saunders*, 10 Jul 1898 (PH). Sullivan Co.: Lincoln Falls, *Johnson*, 6 Jul 1924 (PH). Wayne Co.: SE of Scott Center, *Wherry*, 3 Sep 1939 (PH). RHODE ISLAND.—Providence Co.: Diamond Hill, *Palmer* 46746 (US). SOUTH DAKOTA.—Meade Co.: Piedmont & Little Elk Creek, *Rydberg* 1198 (US). TENNESSEE.—Blount Co.: SE of Walland, *Wherry*, 9 Jun 1934 (PH). UTAH.—Grand Co.: Post Canyon, *Graham* 9876 (US). Piute Co.: Marysvale, *Jones* 5896 (US). Sanpete Co.: Lake Canyon, Manti, *Tidestrom* 1872 (US). Washington Co.: Zion National Park, *Pennell & Schaeffer* 21682 (PH). VERMONT.—Chittenden Co.: Huntington, *Doray*, Jul 1943 (US). Rutland Co.: Brandon, *Knowlton*, 20 Aug 1899 (US). Washington Co.: Duxbury, *Doray*, 30 Jun 1944 (US). Windham Co.: Townshend, *Wheeler*, 16 Sep 1922 (S-PA). Windsor Co.: Quechee Gulf, *Leeds* 772 (PH). VIRGINIA.—Fauquier Co.: Marlsham, *Allard* 2885 (US). Madison Co.: Stony Man Mt., *Palmer*, 26 Aug 1901 (US). Page Co.: Mount Marshall, *Allard* 771 (US). WASHINGTON.—Asotin Co.: SW of Anatone, *Cronquist* 5716 (S-PA, US). Cowlitz Co.: Castle Rock, *Kellogg & Hartford* 1185 (US). Kittitas Co.: Mt. Stuart, *Thompson*, 16 May 1931 (PH). Okanogan Co.: Muckamuck Lookout, *Thompson* 6992 (PH). Pierce Co.: Eagle Peak, Mt. Rainier National Park, *Jennings* 10011 (US). Skamanis Co.: Mt. St. Helens, *Coville* 825 (US). Whatcom Co.: Chuckanut Drive, *Thompson* 5910 (PH). Yakima Co.: Yakima Region, Snipes Creek, *Cotton* 422 (US). WEST VIRGINIA.—Hardy Co.: 7 mi. N of Moorefield, *Wherry*, 12 Apr 1936 (PH). WYOMING.—Albany Co.: 11 mi. E of Laramie, *Wherry*, 9 Jun 1937 (PH). Fremont Co.: Farson-Lander Road, *Porter* 4980 (PH). WISCONSIN.—Trempealeau Co.: Perrot State Park, *Hartley*, 8 Jun 1956 (US). Sauk Co.: near Merrimac, *Wherry & Leeds* 3303 (PH).

SOUTH AMERICA

ARGENTINA.—Nord-Patagonien, San Carlos, *Buchtien* 174 (S-PA). Santa Cruz, Lago Argentino, *Vervoorst* 4379 (S-PA). Neuquen, Arroyo La Estacada, *Barba* 2160 (US). Rio Negro, Cerro Catedral, *Pedersen* 1471 (US). Lago Correntoso, *Pedersen* 229 (US). BOLIVIA.—Ornro, Abaroa, Challapata, *Asplund* 3247 (S-PA). La Paz, Omasngas, Isla del Sol. Yumani, *Asplund* 3617 (S-PA). Pelichuco, *Williams* 2614 (US). Insel Titicaca, *Buchtien* 2804 (US). CHILE.—Valparaiso, Salto-Islen, *Skottsberg* 933 (S-PA). Temuco, *Claude-Joseph* 1893 (US). Santiago, above Rio Colorado. *Hastings* 513 (US). Valdivia, *Buchtien*, Dec 1896 (US). COLOMBIA.—Narino, 6 kilom. above San Jose, *Ewan* 16571 (US). Santander, near Vetas, *Killip & Smith* 17950 (US). Boyaca, Hacia La Cueva, *Cuatrecasas* 1627 (US). ECUADOR.—El Carchi, El Angel, *Popenoe*, Jun 1921 (US). Pichincha, 5-6 mi. W of Quito, *Steyermark* 52380 (US). JUAN FERNANDEZ.—Mas Afuera, *Skottsberg* 508 (S-PA, US). PERU.—between Juliaca and Cuzco, *Hitchcock* 22440 (US). Arequipa, Lomas de Capac, *Coronado* 40 (US). Puno, Caccarhara, *Pearson* 105 (PH). VENEZUELA.—Merida, Laguna Mucubaji, *Steyermark* 57491 (US).

EURASIA

CHINA.—Shansi, Lu Yah Shan, *Smith* 8134 (S-PA).

CZECHOSLOVAKIA.—Bohemia, Gratzen, *Jaky*, 16 Aug. 1893 (S-PA).

DENMARK.—Lolland, *Lange*, 4 Jun 1848 (S-PA); Moen, Vollerrip, *Ingerster*,

12 Aug 1897 (S-PA). The Faeroes.: Island of Astero, *Simmons*, 17 Aug 1895 (S-PA); Island of Sudero, Vag, *Simmons*, 17 Aug 1895 (S-PA).

FRANCE.—Haute Savoie, Mt. Vergy, *Boissier*, Jul 1859 (S-PA). Savoy, la Thouviere pres Tignes, *Chermezon & Evrarad*, 21 Aug 1913 (P). Pyrenees Orientales, Collioure, *Copineau*, 20 May 1891 (P). Ain, E du Reculet, *Pfister* 1081 (US). Cantal, Vallee du Sinica, *Walter* 459 (P, US). Haute Savoie, Chamonis, *Rey-Pailhade*, n.d. (P). Nievre, Montsauche, *Duffour*, 2 Jun 1915 (P). Mondoubleau (Loir-et-Cher), Sarge, *Desvaux*, 24 May 1848 (P). Haute Saone, Fleurey-le-Faverney, *Bertrand*, Sep 1889 (P). Seine-et-Oise, Magny pres Chateaufort, *Guillotaux*, 12 Jun 1848 (S-PA).

GERMANY.—Baden, Heidelberg, *Lang*, 17 Sep 1869 (S-PA). Sachsen, Lohmen, *Kohl*, 1872 (S-PA); Eisleben, *Eggers*, 27 Aug 1907 (S-PA). Hannover, *Wappenley*, Aug 1866 (S-PA). Mecklenburg, Babelin, *Hahn*, Jun 1906 (S-PA). Brandenburg, Guben, *Baenitz*, n.d. (S-PA).

HUNGARY.—Tozsony, *Baumler*, Sep 1910 (S-PA). Gomor, Murany, *Richter*, 5 Jul 1901 (S-PA).

IRAN.—Khorasan, Mts. of Nishapur, *Gauba*, 23 Jul 1937 (S-PA).

ITALY.—S. Tirol, Mts. of Merano, *Enander*, 10 Sep 1925 (S-PA). Etrusca (Tuscany), *Agosto*, 1862 (S-PA).

LEBANON.—Mizrab supre Arz Er Rab (Cedros), *Samuelsson*, 10 Jun 1932 (S-PA).

NETHERLANDS.—Valkenburg, Zuid-Limburg, *Lako*, Aug 1903 (S-PA).

NORWAY.—Sondhordl, Bommelon, *Andersson*, 13 Jul 1891 (S-PA). Asker, *Vestergren*, 12 Jul 1916 (S-PA).

POLAND.—Bromberg (Bydgoszcz), *Baenitz*, 1864 (S-PA). Sommerfeld (Zemsz), *Baenitz*, Jul 1859 (S-PA).

PORTUGAL.—Sierra da Estrella, *Birger*, 5 Apr 1921 (S-PA). Porto, *Buchtien*, 1891 (US).

SPAIN.—Leon Pena Coroida, *Gandoger*, Jun 1904 (L). Lerida, Monsech de Rubies, *Kretschmer*, 28 May 1926 (S-PA). Navarre, regiou of Aragon River, *Enander*, 1 Oct 1927 (S-PA).

SWEDEN.—Varmland, Sunne, *Ohlin*, 30 Jul 1920 (S-PA). Stockholm, Runmaro, *Rosendahl*, Jul 1915 (S-PA). Lappland, Jukkasjarvi, *Smith*, 6 Jul 1927 (L, S-PA). Jamtland, Areskutan, *Rosendahl*, 20 Jul 1910 (S-PA).

SWITZERLAND.—Interlaken, *Birger*, 23 Jun 1925 (S-PA). Luzern, Sonnenberg, *Birger*, 23 May 1925 (S-PA). Lugano, *Birger*, 12 Jun 1925 (S-PA). Bern, Kandersteg, *Tavel*, 27 Aug 1916 (S-PA). Valais, Erbignon, *no coll.* (US). Gimmelswald, *Keller*, 9 Jul 1893 (PH).

SYRIA.—Arissa, *Ehrenberg*, May-Jun 1820-26 (L). Mont Amanus, *Haradjian*, Aug 1906 (S-PA). Berut, *Ehrenberg*, 18 May 1824 (S-PA).

UNION OF SOVIET SOCIALIST REPUBLICS.—Lapponia murmanica, Rynda, *Hulten*, 1 Aug 1927 (S-PA). "Iter Ircutense ad fl. Lena et Kirenga," *Kusnezow*, 1910 (S-PA). Moskau, Kunzowo, *Balezunw*, 9 Jul 1901 (S-PA). Estonia, Ostseeinsel Dago bei Tardas, *Kupffer*, 8 Aug 1903 (S-PA); Wormso, Magnushof, *Gröntved*, 15 Jul 1926 (S-PA). Livland, Osteeinsel Ösel, *Kupffer*, 10 Aug 1907 (S-PA). Kamtchatka.: Lake Asabatch, *Malaise*, Aug 1925 (S-PA); Bolschajas flodsystem, *Hulten*, 12 Sep 1921 (S-PA); near Petropavlovsk, *Mertius*, n.d. (S-PA); Savoiko, *Eyerdam*, 27 Jul 1928 (S-PA).

AFRICA AND ASSOCIATED ISLANDS

AZORES.—Tayal, *Brown* 328 (PH, US).

BELGIAN EAST AFRICA.—Mt. Kenia, *Mearns* 1442 (US).

CANARY ISLANDS.—Gran Canaria, *Rosendahl*, Jan 1913 (S-PA). Tenerife, Agua Garcia, *Cyren*, 12 Jun 1929 (S-PA).

MADEIRA.—Funchal, *Bornmuller*, 22 Mar 1900 (S-PA).

MOROCCO.—Azib de Tiebka, *Balls B2568* (S-PA).

5. *Cystopteris diaphana* × *protrusa* complex

SPECIMENS EXAMINED:

GEORGIA.—Gilmer Co.: 8 mi. E of Chatsworth, *Pyron & McVaugh* 2955 (US). ILLINOIS.—Richland Co.: 2½ mi. N. of Olney, *Ridgway*, 7 Jul 1910 (US). INDIANA.—Howard Co.: 1 mi. E of Burlington, *Deam* 56983 (PH). Parke Co.: 3 mi. SE of Mansfield, *Tryon* 4289 (TENN, US). Wells Co.: Chester Twp., *Deam*, 26 Jun 1904 (US). IOWA.—Poweshiek Co.: Grinnell, *no coll.* (TENN). Winneshiek Co.: ¾ mi. W of Decorah, *Wherry*, 1 Jun 1937 (PH). KENTUCKY.—Graves Co.: 2½ mi. NE of Water Valley, *Wherry*, 11 Jul 1935 (PH). Hardin Co.: Vertrees, *Wherry & Pennell* 13632 (PH). LOUISIANA.—West Feliciana Co.: 1 mi. W of Plettenberg, *Correll* 10472 (US). MICHIGAN.—Van Buren Co.: 2½ mi. E of Bangor on M-43, Hagenah 1372 (US). MISSOURI.—Harrison Co.: near Eagleton, *Palmer & Steyermark* 41350 (PH). Reynolds Co.: Centerville, *Eggert*, 22 Jun 1879 (US). NEBRASKA.—Saunders Co.: Ashland, *Williams*, 18 Aug 1888 (US). NORTH CAROLINA.—Ashe Co.: S of Jefferson, *Wherry*, 14 Jul 1936 (PH). Haywood Co.: Waynesville, *Barksdale*, 1 Aug 1936 (PH). Jackson Co.: Saco Falls, 2 mi. SW Saco Gap, *Anderson* 1446 (PH). NEW MEXICO.—Lincoln Co.: above Ruidoso Creek, *Wilkens* 2365 (PH). OHIO.—Franklin Co.: Columbus, *no coll.* (PH). Lorain Co.: Oberlin, *Grover*, 10 Jul 1900 (US). Trumbull Co.: NE of Brookfield, *Whittenberger*, 10 Sep 1939 (PH). OKLAHOMA.—Murray Co.: Arbuckle Mts., Davis, *Emig* 467 (US). PENNSYLVANIA.—Franklin Co.: Mercersburg, *Porter*, 20 May 1845 (PH). TENNESSEE.—Bradley Co.: below road from Benton Station to Charleston, *Shaver* 10228 (TENN). Cannon Co.: 8 mi. NE of Woodbury, *Shaver* 10206 (TENN). Cumberland Co.: 3 mi N of the Bledsoe Co. line, *Shaver* 10225 (TENN). Grainger Co.: 6 mi. E of the Claiborne Co. line, *Shaver* 10211 (TENN). Hamilton Co.: N of Red Bank, *Shaver* 10633 (TENN). McNairy Co.: S of Selmer, *Shaver* 10204 (TENN). Moore Co.: N of Lynchburg, *Shaver* 10447 (TENN). Unicoi Co.: Bluff near Unaka Springs, *Shaver* 10380 (TENN). Van Buren Co.: E. of Spencer, *Shaver* 10575 (TENN). VIRGINIA.—8 mi. SW of Jonesville, *Wherry*, 11 Jul 1938 (PH). Smyth Co.: near Marion, *Britton & Vail*, 13 Jun 1892 (PH). WEST VIRGINIA.—Cabell Co.: Pleasant Valley, *Gilbert* 860 (PH, TENN). Fayette Co.: *Nuttall*, 1890-98 (PH). Monongalia Co.: Cheat River, Morgantown, *Hatry*, 6 Jul 1902 (PH). Wirt Co.: 1 mi. above Palestine, *Bartholomew* W1941-1035 (TENN).

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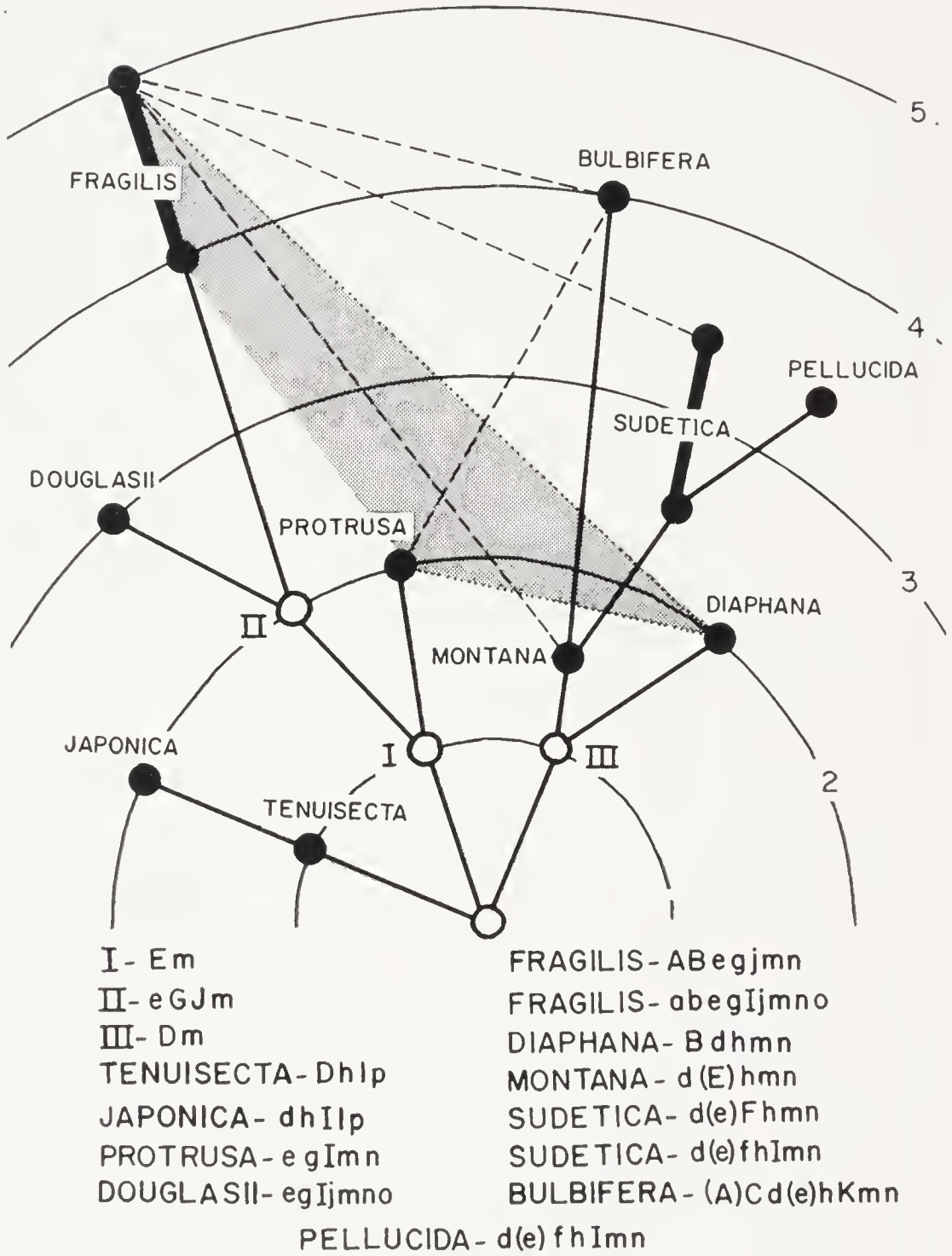

PLATE 1

EVOLUTIONARY TENDENCIES IN *CYSTOPTERIS*

Black dots are species, open circles presumed ancestral types. Solid lines indicate paths of evolution, dashed lines represent allopolyploids, and shaded region indicates taxa which are involved in apparent introgression. Upper case letters show the first occurrence of an advanced character in an evolutionary line; lower case letters indicate subsequent occurrence of advanced characters in the lines. Letters in parentheses represent intermediate conditions.

Characters. A. Rhizome organization. B. Blade pattern. C. Blade attenuation. D. Vein position. E. Adaxial epidermal cell wall outline. F. Scales with lateral cell wall thickenings. G-H. Indusial cells (No obvious trend). G. Attenuate. H. Short. I. Glandularity of indusium. J. Accessory indusial hairs. K. Foliar bulblets. L-M. Multicellular hairs (No obvious trend). L. Non-glandular. M. Glandular. N-P. Spore architecture (No obvious trend). N. Echinate. O. Rugose. P. Spines with irregular cross sections.

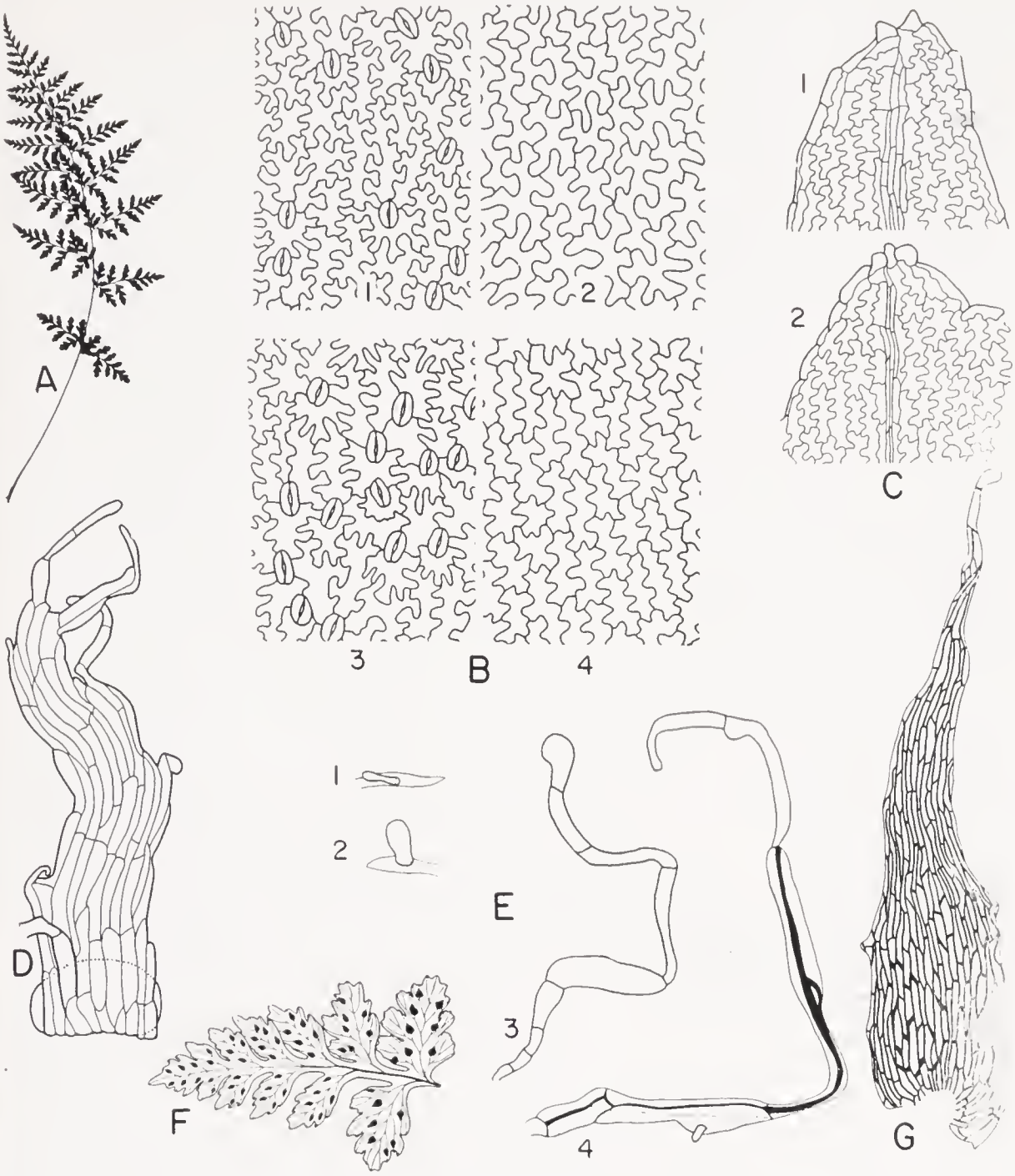

PLATE 2

CYSTOPTERIS FRAGILIS (L.) BERNH.

Fig. A. Silhouette of blade. Germany, Merxmüller, Aug. 1956. (living material. Grown at U. of Michigan Botanical Gardens). B. Epidermal cells. 1-2. Greenland, *Bartlett* 459*a* (US). 3-4. Sadlerochit River, Alaska, *Spetzman* 1184 (US). C. Marginal laminar cells. 1. Fort Yukon, Alaska, Russell, 8-12 Aug. 1889 (US). 2. Vicinity of Cape Lisburne, Alaska, *Washburne*, Jul. 1904 (US). D. Indusium. Fort Yukon, Alaska, Russell, 8-12 Aug. 1889 (US). E. Hairs and hair-like scales. F. Pinna. Sadlerochit River, Alaska (US). G. Scale of rhizome. Northwest Territories, Canada, *Porsild* 5194 (S-PA). The scale of each drawing is indicated on Plate 3.

PLATE 3

CYSTOPTERIS PROTRUSA (WEATH.) BLASDELL

Fig. A. Silhouette of blade. Near Chelsea, Michigan, *Blasdell* 277. B. Epidermal cells. 1-2. Near Chelsea, Michigan, *Blasdell* 277. C. Marginal laminar cells. Sulphur Springs, Pennsylvania, *Berkimer* 1254 (PH). D. Indusium. Near Chelsea, Michigan, *Blasdell* 277. E. Hairs. F. Pinna. Dexter Township, Michigan, *Wagner* 8075 (MICH). G. Scale of rhizome. Nolan, West Virginia, *Wherry*, 12 Jul. 1938 (PH).

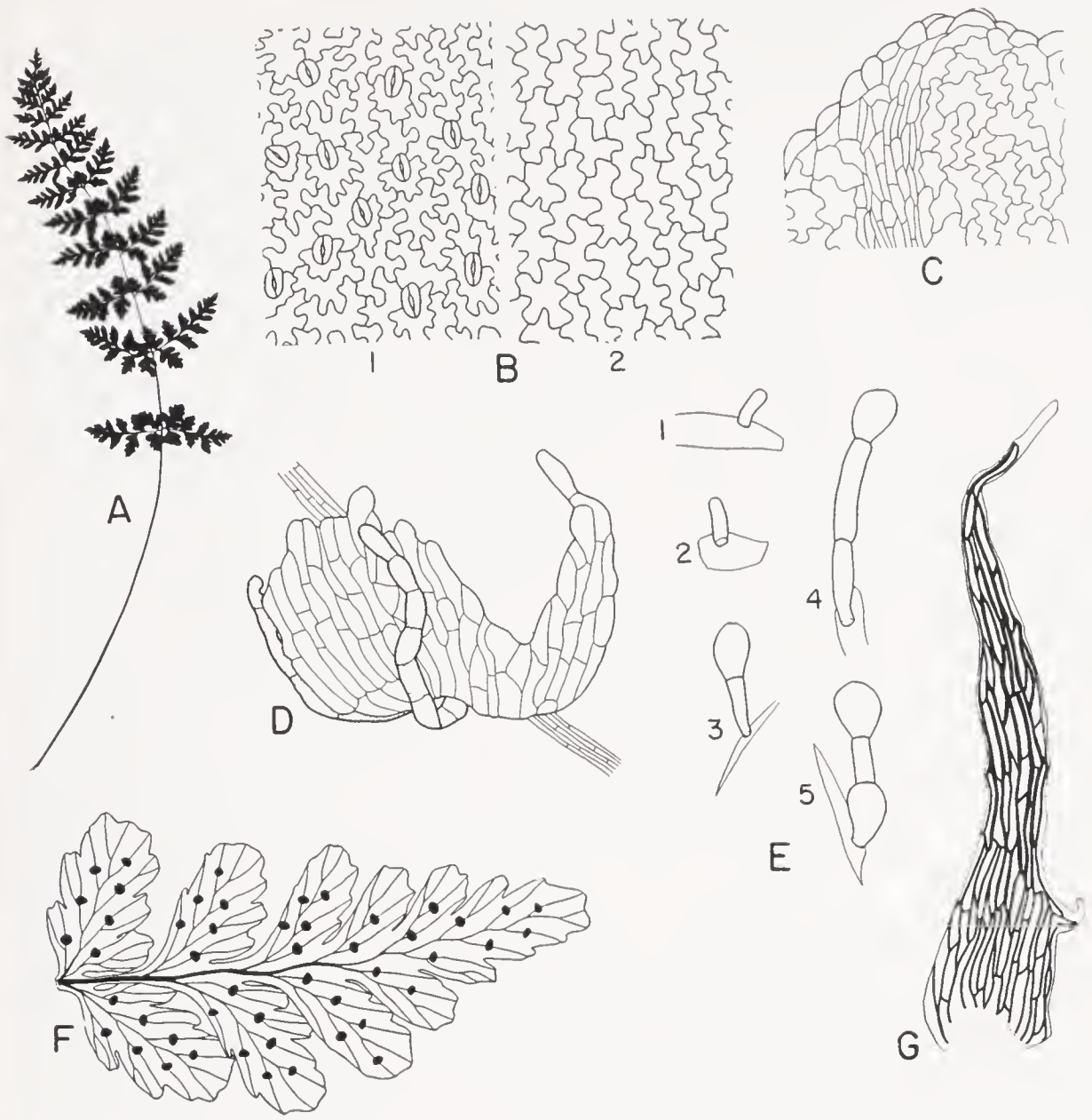

PLATE 4

CYSTOPTERIS DOUGLASII HOOK.

Fig. A. Silhouette of blade. Mauna Kea, Hawaii, *Horner*, 31 Jul. 1956 (from plants grown at the U. of Michigan Botanical Gardens). B. Epidermal cells. Hawaii, *Baldwin*, n.d. (PH). C. Marginal laminar cells. Haleakala Crater, Maui, T. H., *Hitchcock* 14966 (US). D. Indusium. Maui, Hawaii, *Mann & Brigham* 480 (US). E. Hairs. F. Pinna. Maui, Hawaii, *Mann & Brigham* 480 (US). G. Scale of rhizome. Haleakala Crater, Maui, *Wagner* 5261 (UC). The scale of each drawing is indicated on Plate 3.

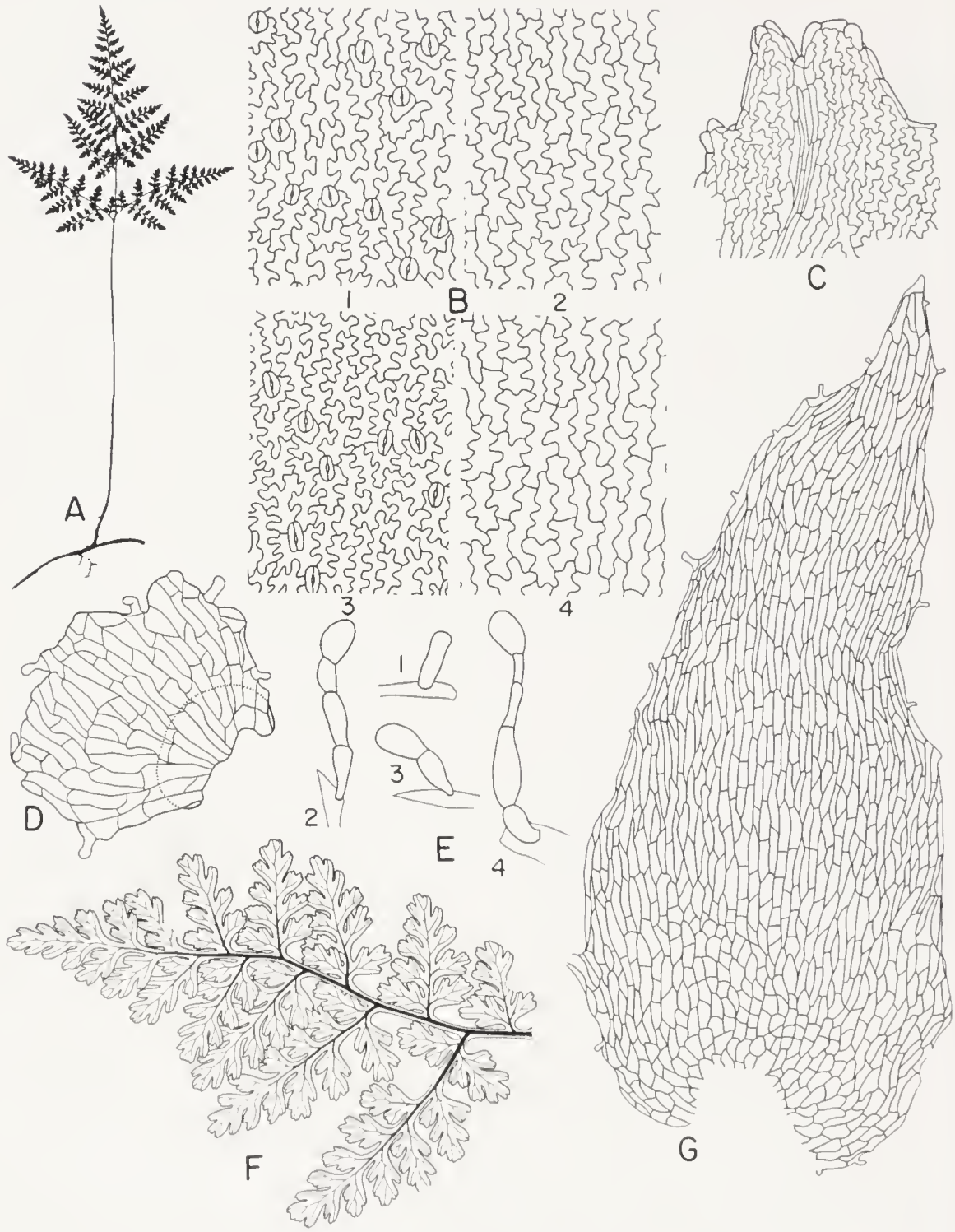

PLATE 5

CYSTOPTERIS MONTANA (LAM.) *BERNH.*

Fig. A. Silhouette of blade. Tyndero, Norway, *Blomquist*, 16 Aug. 1936 (S-PA). B. Epidermal cells. 1-2. Fish Lake, British Columbia, *Shaw* 1210 (US). 3-4. Yukon River, Alaska, *Palmer* 70 (US). C. Marginal laminar cells. Swiss Tyrol, Langkofll, *Macfarlane*, 9 Jul. 1906 (PH). D. Indusium. Yukon River, Alaska, *Palmer* 70 (US). E. Hairs. F. Pinna. Nome, Alaska, *Powers* 90 (US). G. Scale of rhizome. Jamtland, Switzerland, *Osterlind*, 30 Jul. 1935 (US). The scale of each drawing is indicated on Plate 3.

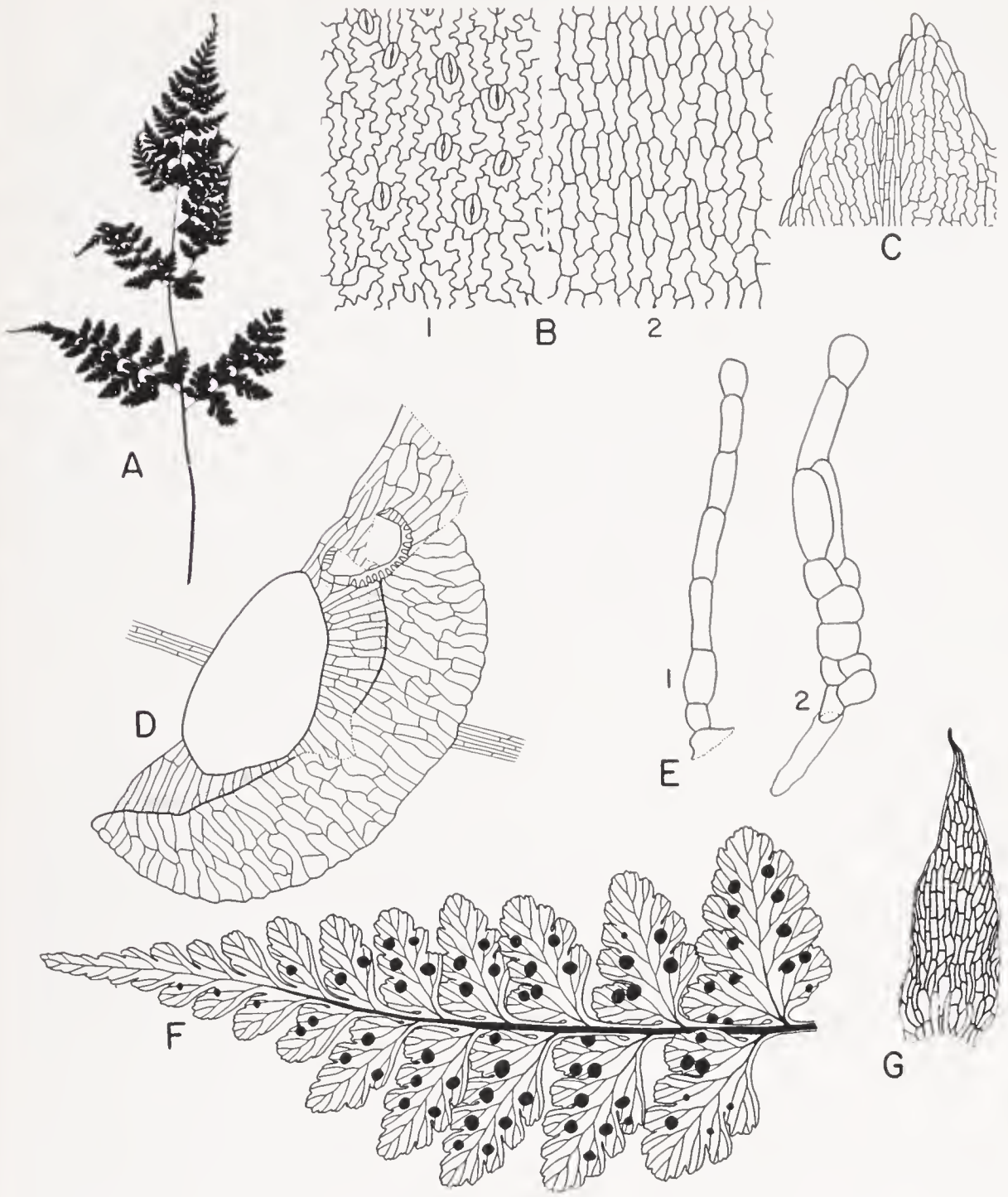

PLATE 6

CYSTOPTERIS PELLUCIDA (FRANCH.) CHING

Fig. A. Silhouette of blade. Yunnan, *Ducloux*, 29 Aug. 1909 (P). B. Epidermal cells. Yunnan, *Ducloux*, 29 Aug. 1909 (P). C. Marginal laminar cells. Yunnan, China, *Delavay*, n.d. (P). D. Indusium. Yunnan, China, *Ducloux*, 29 Aug. 1909 (P). E. Hairs. F. Pinna. Yunnan, China, *Ducloux*, 29 Aug. 1909 (P). G. Scale of rhizome. Yunnan, China, *Delavay*, n.d. (P). The scale of each drawing is indicated on Plate 3.

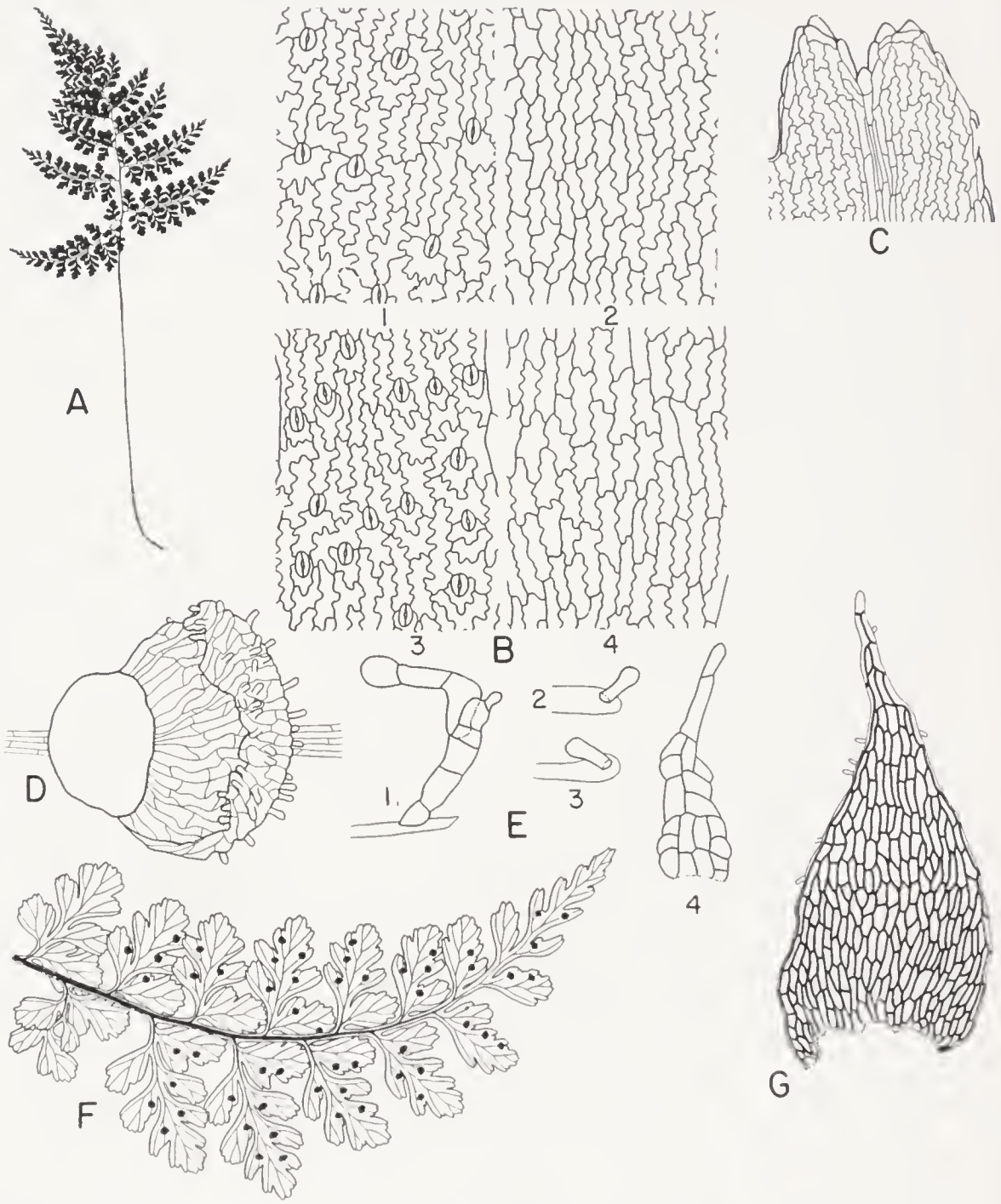

PLATE 7

CYSTOPTERIS SUDETICA A. BR. ET MILDE

Fig. A. Silhouette of blade. Gomor, Hungary, *Richter*, 12 Aug. 1900 (S-PA). B. Epidermal cells. 1-2. *C. sudetica* var. *sudetica*, Moravia, Czechoslovakia, *Laus*, Aug. 1935 (S-PA). 3-4. *C. sudetica* var. *moupinensis*, Szechuan, China, *Smith* 4227 (S-PA). C. Marginal laminar cells. Silesia, Poland, *Laus*, 7 Jul. 1933 (S-PA). D. Indusium. Transylvania, Romania, *Pop*, 29 Aug. 1935 (S-PA). E. Hairs. F. Pinna. Pimninenpass, Hungary, *Ullepitsch*, 20 Jun. 1890 (S-PA). G. Scale of rhizome. Szepes, Hungary, *Gyorffy*, Jul. 1907 (US). The scale of each drawing is indicated on Plate 3.

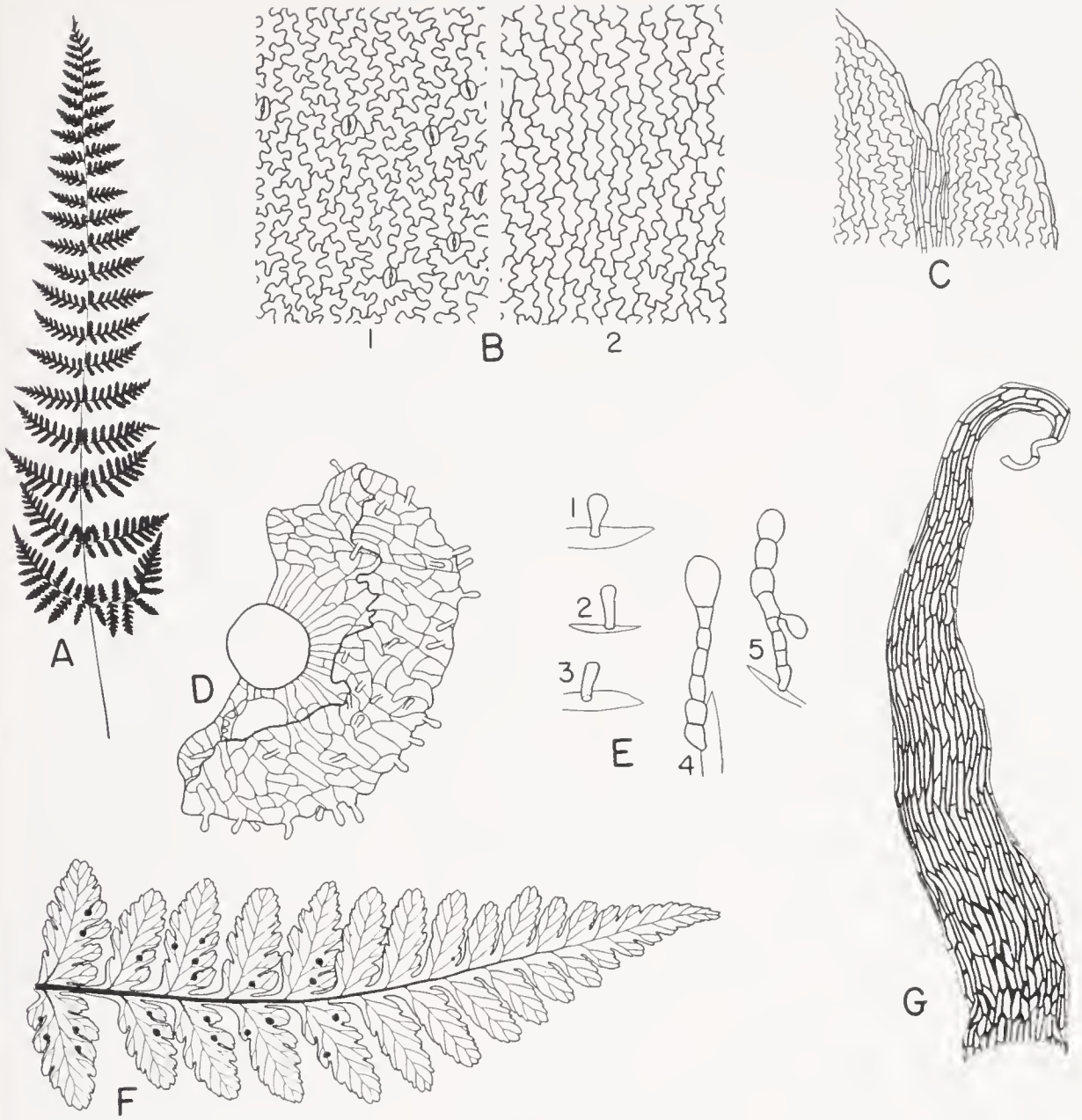

PLATE 8

CYSTOPTERIS BULBIFERA (L.) BERNH.

Fig. A. Silhouette of blade. Becks Woods, near Plymouth, Michigan, *Blasdell*, 18 Jul. 1958 (MICH). B. Epidermal cells. Grand Ledge, Michigan, *Wagner* 8078 (MICH). C. Marginal laminar cells. Oka, Quebec, *Adrien* 1273 (PH). D. Indusium. Ephraim, Wisconsin, *Millspaugh* 3954 (US). E. Hairs. F. Pinna. Grand Ledge, Michigan, *Wagner* 8078 (MICH). G. Scale of rhizome. Grand Ledge, Michigan, *Wagner* 8078 (MICH). The scale of each drawing in indicated on Plate 3.

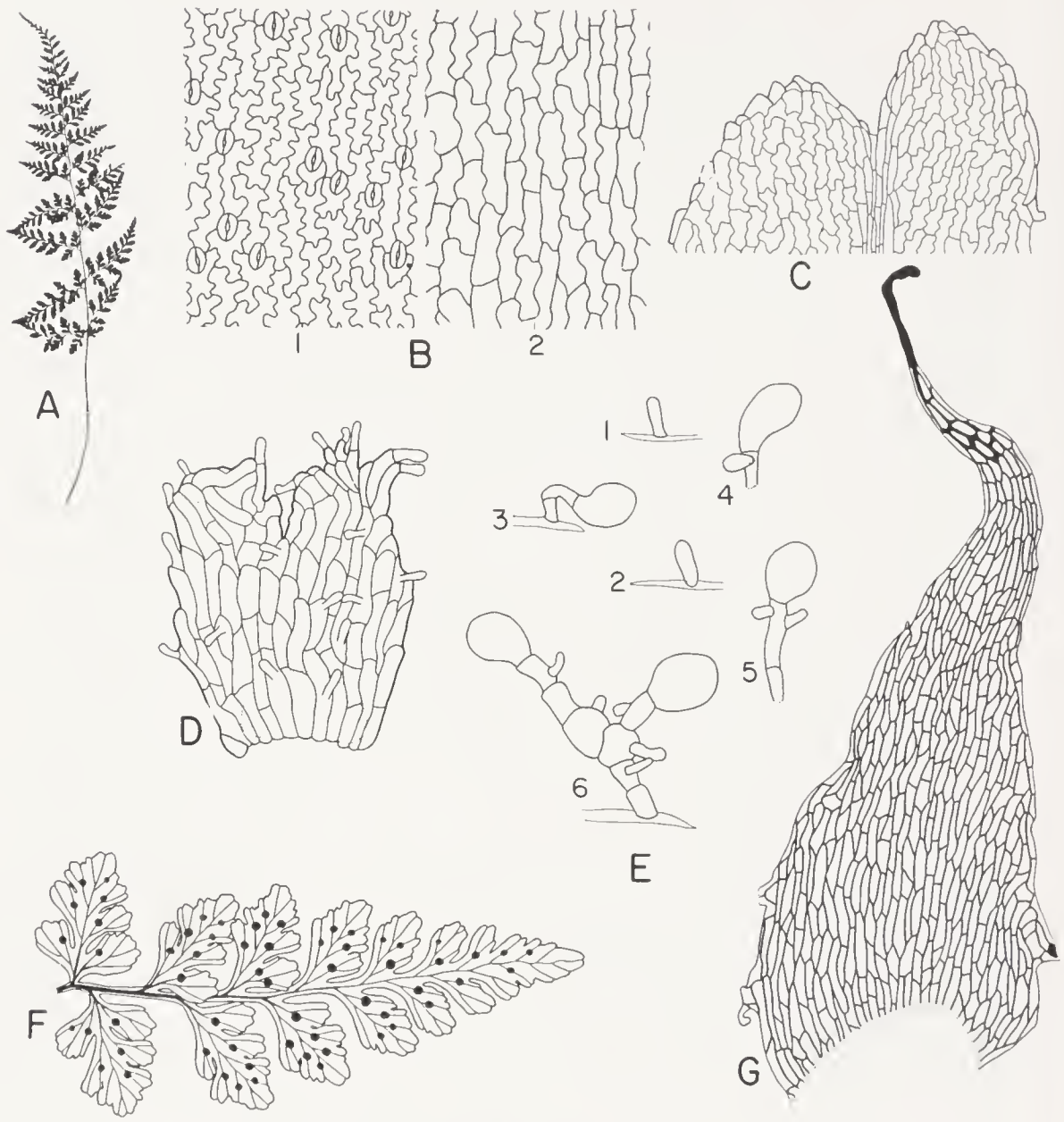

PLATE 9

CYSTOPTERIS DIAPHANA (BORY) BLASDELL

Fig. A. Silhouette of blade. Peru, *Bues* 1004 (US). B. Epidermal cells. Peru, *Bues* 1004 (US). C. Marginal laminar cells. Peru, *Bues* 1004 (US). D. Indusium. Chile, *Joseph* 5591 (US). E. Hairs. F. Pinna. Peru, *Bues* 1004 (US). G. Scale of rhizome. Tucuman, Argentina, *Venturi* 6086 (US). The scale of each drawing is indicated on Plate 3.

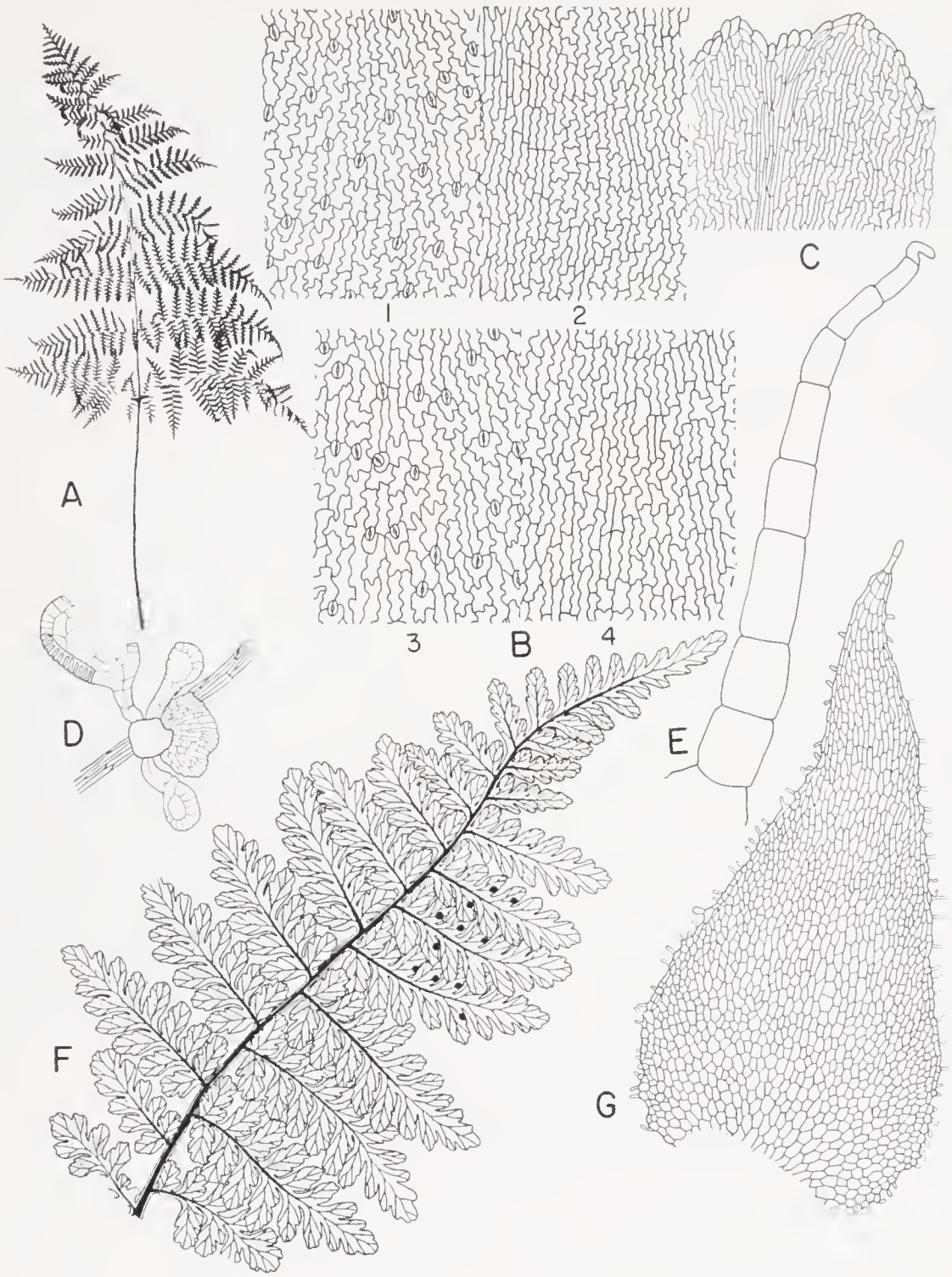

PLATE 10

CYSTOPTERIS JAPONICA LSSN.

Fig. A. Silhouette of blade. Honshu, Japan, *Kurata,* 28 Nov. 1956. B. Epidermal cells. 1-2. Plant with 2n spores. Shikoku, Japan, *Uno* 2611 (US). 3-4. Plant with larger spores. Shikoku, Japan, *n.c.* 11 Jul. 1892 (US). C. Marginal laminar cells. Shikoku, Japan, *n.c.* 11 Jul. 1892 (US). D. Indusium. Shikoku, Japan, *Uno* 2611 (US). E. Multicellular non-glandular hair. F. Pinna. Honshu, Japan, *Kurata,* 28 Nov. 1956. G. Scale from stipe base of young frond. Honshu, Japan, *Kurata,* 28 Nov. 1956. The scale of each drawing is indicated on Plate 3.

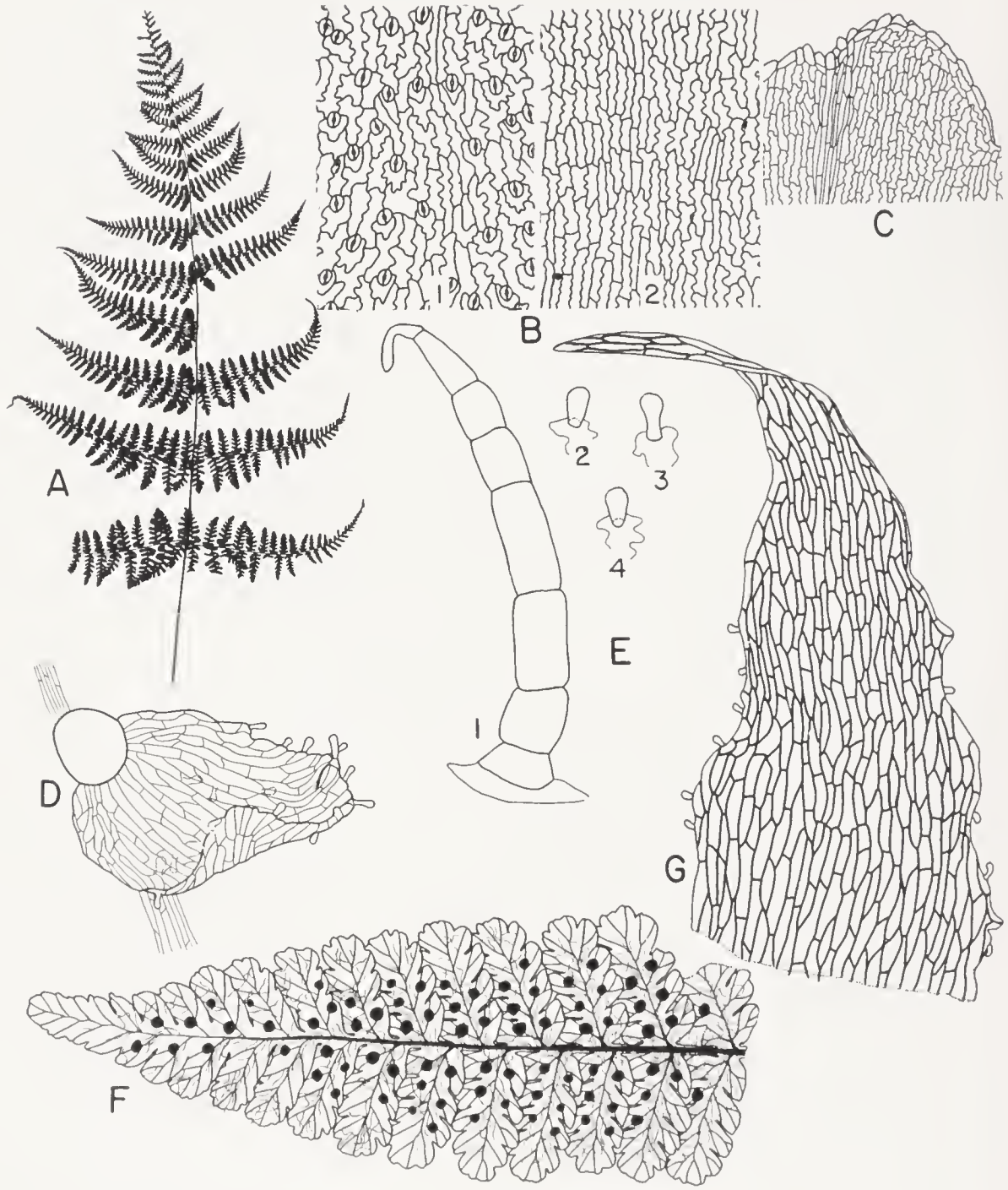

PLATE 11

CYSTOPTERIS TENUISECTA (BL.) METT.

Fig. A. Silhouette of blade. Yunnan, China, *Henry* 11539A (US). B. Epidermal cells. Pahang, Malaya, *Holttum*, 10 May 1936 (US). C. Marginal laminar cells. Assam, *Mann*, Jul. 1890 (S-PA). D. Indusium. Yunnan, China, *Henry* 11539A (US). E. Hairs. 1. Multicellular non-glandular hair. 2-4. Unicellular glandular hairs. F. Pinna. Assam, *Mann*, Jul. 1890 (S-PA). G. Scale of rhizome. Assam, *Mann*, Jul. 1890 (S-PA). The scale of each drawing is indicated on Plate 3.

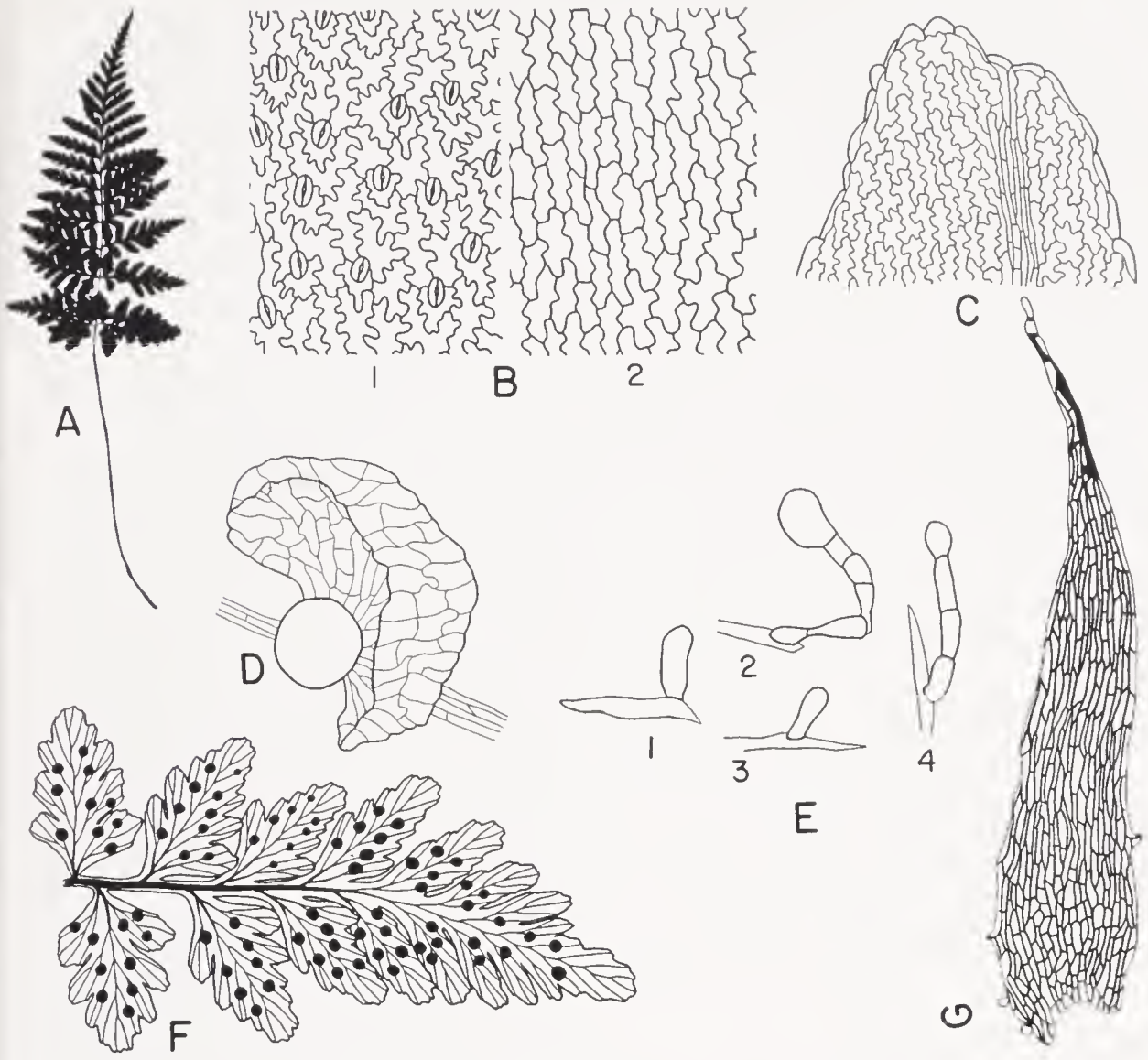

PLATE 12

CYSTOPTERIS X TENNESSEENSIS SHAVER

Fig. A. Silhouette of blade. Marshall Co., Tennessee, *Shaver* 10460 (US). B. Epidermal cells. Martin's Bluff, Arkansas, *McGregor* 3722 (US). C. Marginal laminar cells. Johnson Co., Kansas, *McGregor* 4389 (US). D. Indusium. Livingston, Tennessee, *Shaver* 10553 (TENN). E. Hairs. F. Pinna. *McGregor* 3722. G. Scale of rhizome. Neodesha, Kansas, *McGregor* 3404 (US). The scale of each drawing is indicated on Plate 3.

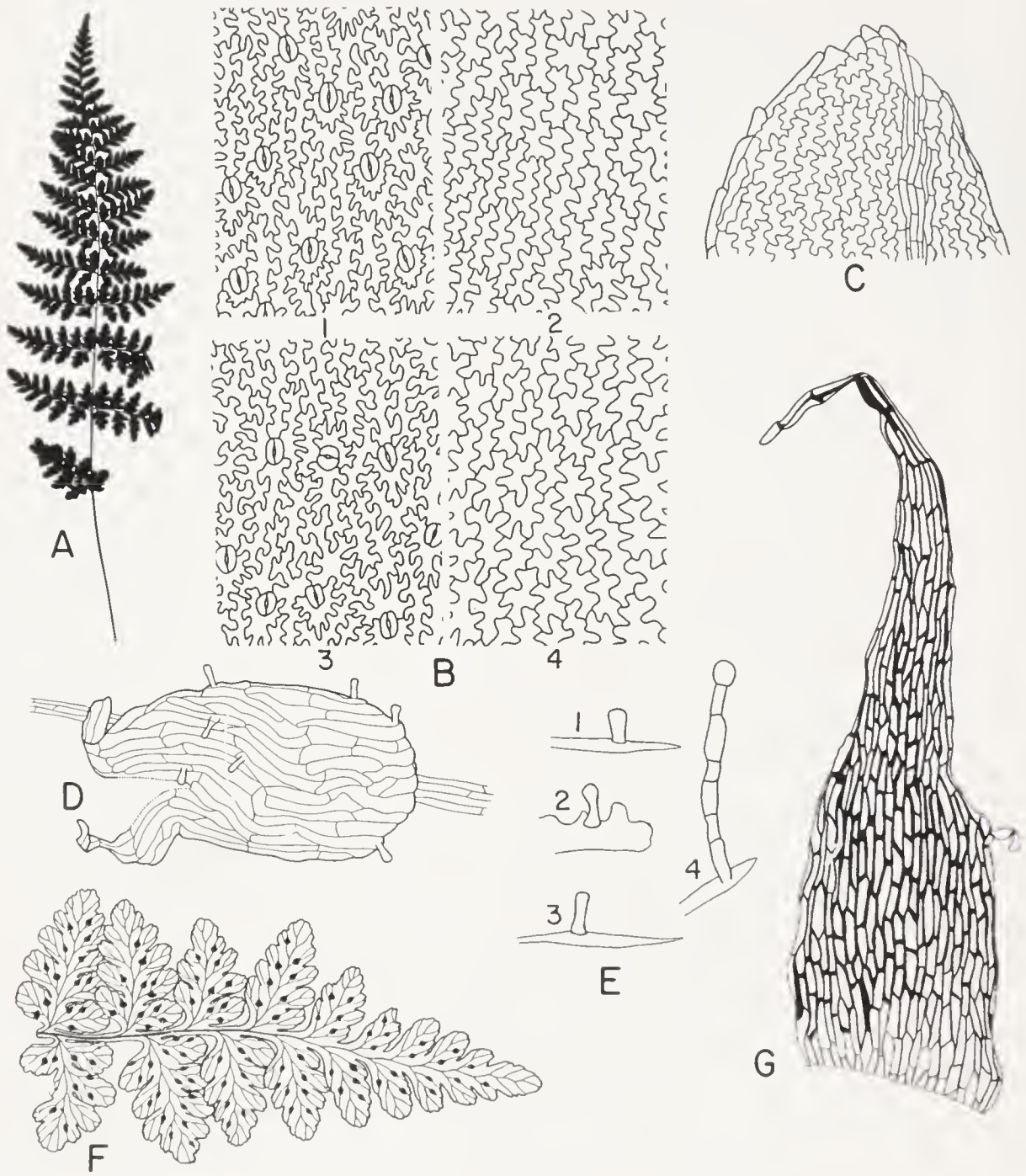

PLATE 13

CYSTOPTERIS X LAURENTIANA (WEATH.) BLASDELL.

Fig. A. Silhouette of blade. Amnicon Falls, Wisconsin, *Tryon* 4874 (US). B. Epidermal cells. Fayette, Michigan, *Hagenah*, 19 Jul. 1954 (MICH). 1-2. Plant with normal spores. 3-4. Plant with aborted spores and possibly a backcross to *Cystopteris fragilis*. C. Marginal laminar cells. Lake Co., Minnesota, *Tryon & Faber* 4896 (US). D. Indusium. Bic, Quebec, *Rousseau* 26549 (US). E. Hairs. F. Pinna. Bruce Peninsula, Ontario, *Taylor* 6129 (US). G. Scale of rhizome. *Taylor* 6129. The scale of each drawing is indicated on Plate 3.

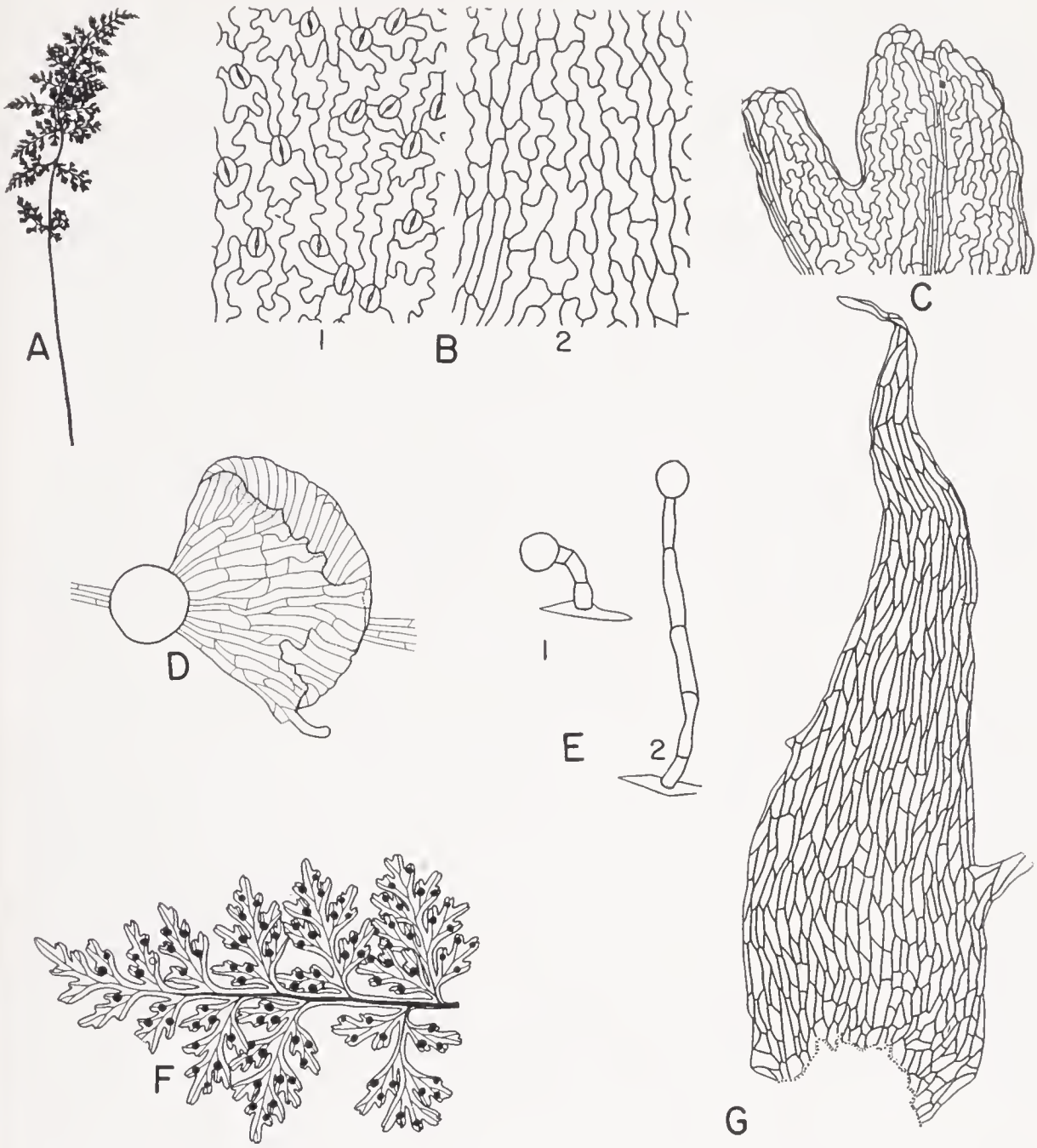

PLATE 14

CYSTOPTERIS X ALPINA (WULFEN) DESV.

Fig. A. Silhouette of blade. Bavarian Alps, Germany, *Shultes* (L). B. Epidermal cells. Carinth, Switzerland, *Suringar*, 1865 (L). C. Marginal laminar cells, *Suringar*, 1865. D. Indusium. *Savoye*, Switzerland (L). E. Hairs. F. Pinna. *Suringar*, 1865. G. Scale of rhizome. Savoy, France, *Bourgeau*, 27 Jul. 1873 (L). The scale of each drawing is indicated on Plate 3.

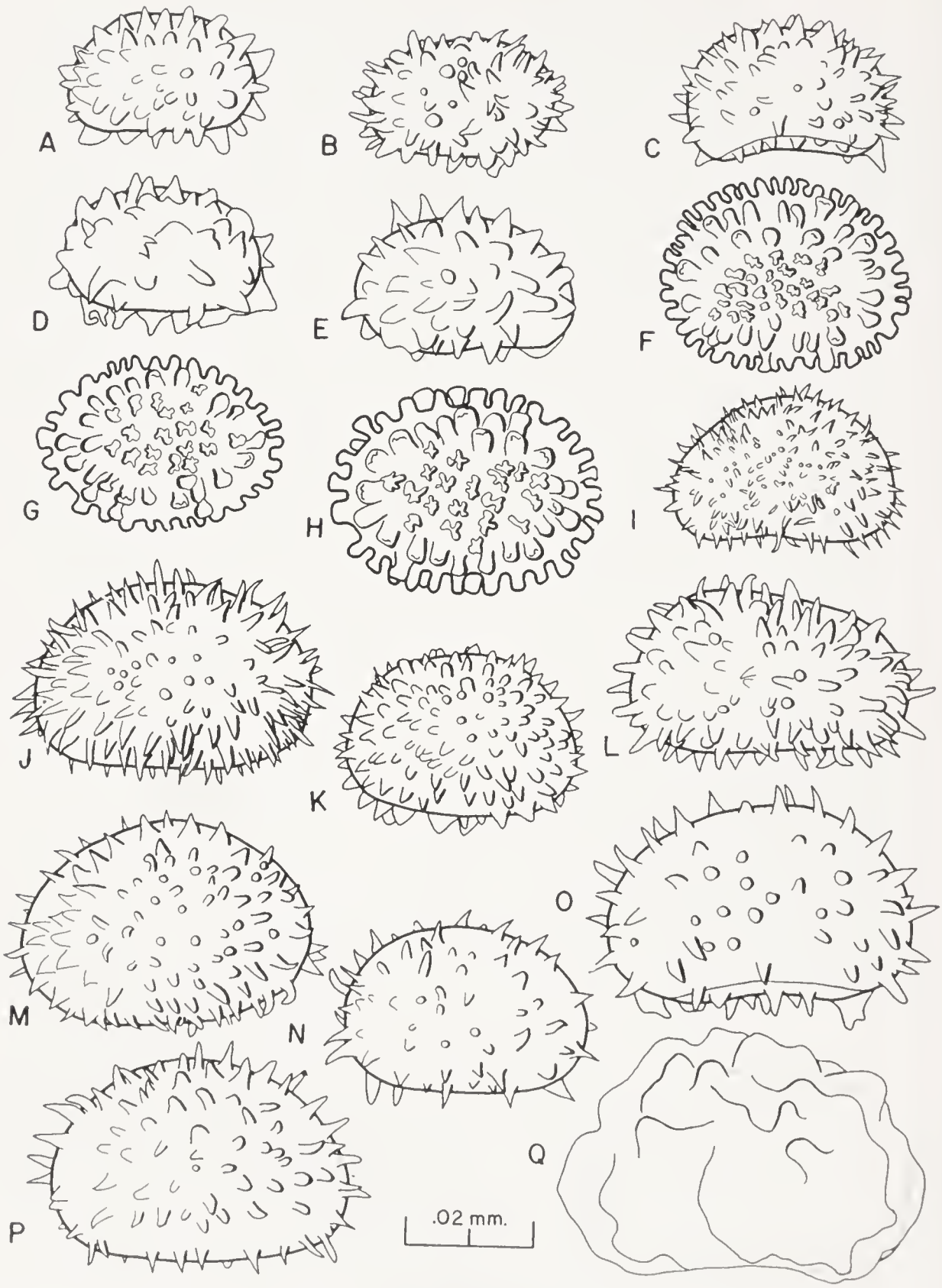

PLATE 15

SPORES IN *CYSTOPTERIS*

Fig. A. *C. bulbifera.* B. *C. protrusa.* C. *C. sudetica.* D, E. *C. montana.* F. *C. tenuisecta.* G, H. *C. japonica.* I, J. *C. diaphana.* K. *C. X tennesseensis.* L, M. *C. X laurentiana.* N, P. *C. fragilis.* O. *C. douglasii.* Q. *C. fragilis* (rugose spore).

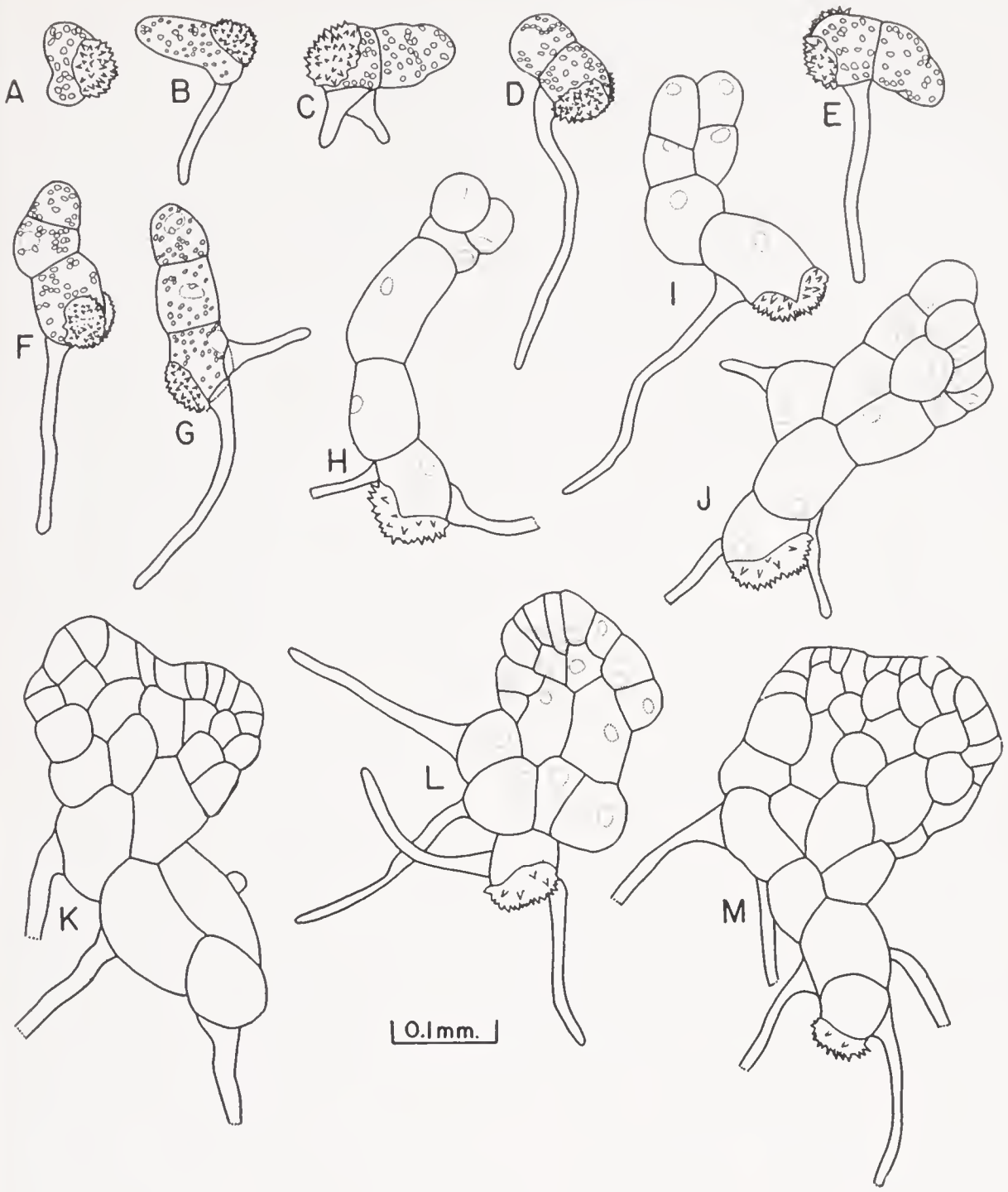

PLATE 16

GAMETOPHYTE DEVELOPMENT IN *CYSTOPTERIS*

Gametophytes of *C. douglasii*. Fig. A-G. Filamentous stage. H-M. Cell plate stage.

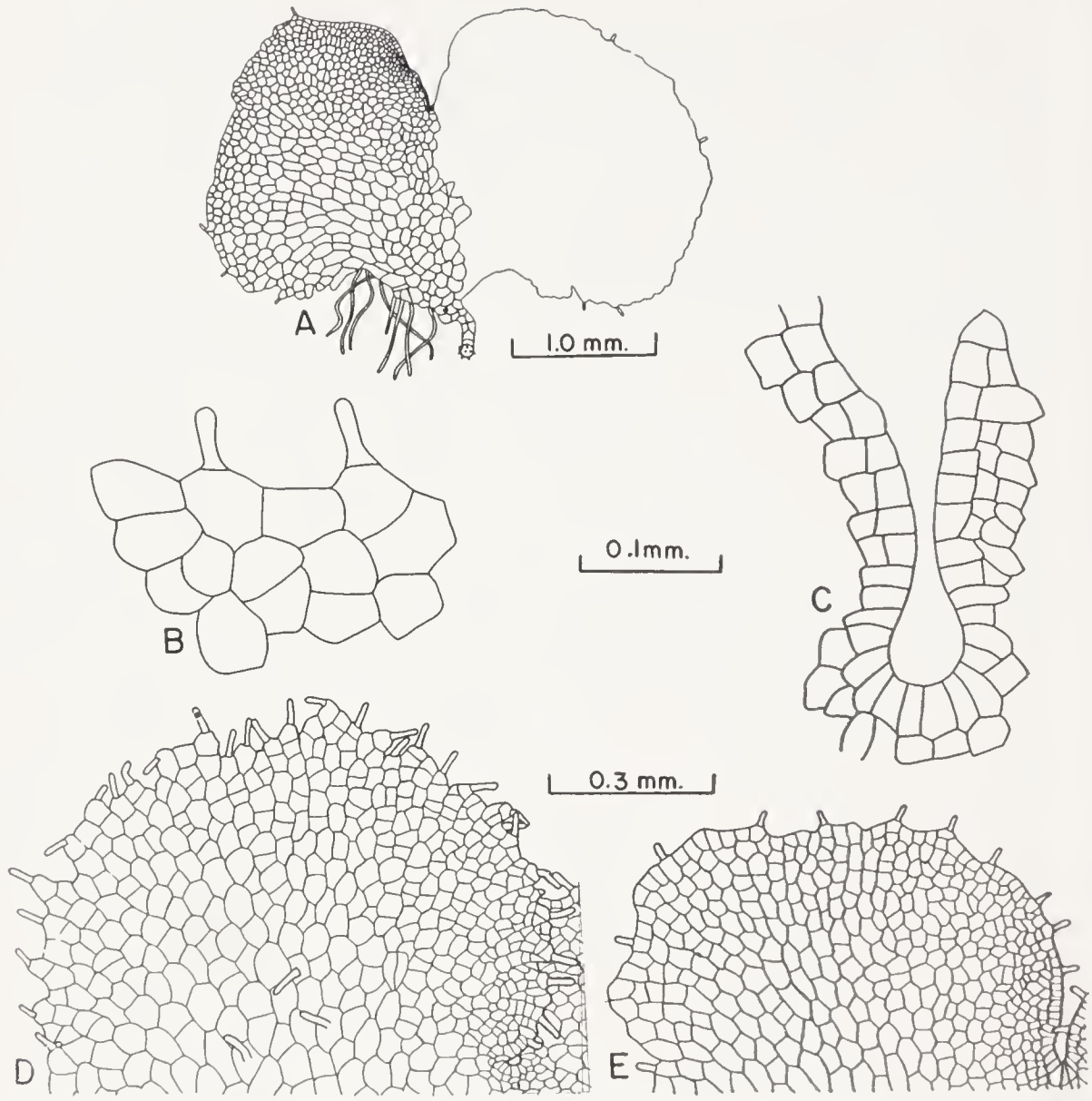

PLATE 17

MATURE GAMETOPHYTE IN *CYSTOPTERIS*

Fig. A. Gametophyte of *C. douglasii*. B. Detail of marginal cells and glands. *C. douglasii*. C. Detail of gametophyte notch. *C. douglasii*. D. Lobe of *C. diaphana* gametophyte showing irregular margin and long glands. E. Lobe of *C. fragilis* gametophyte showing smooth margin and shorter glands.

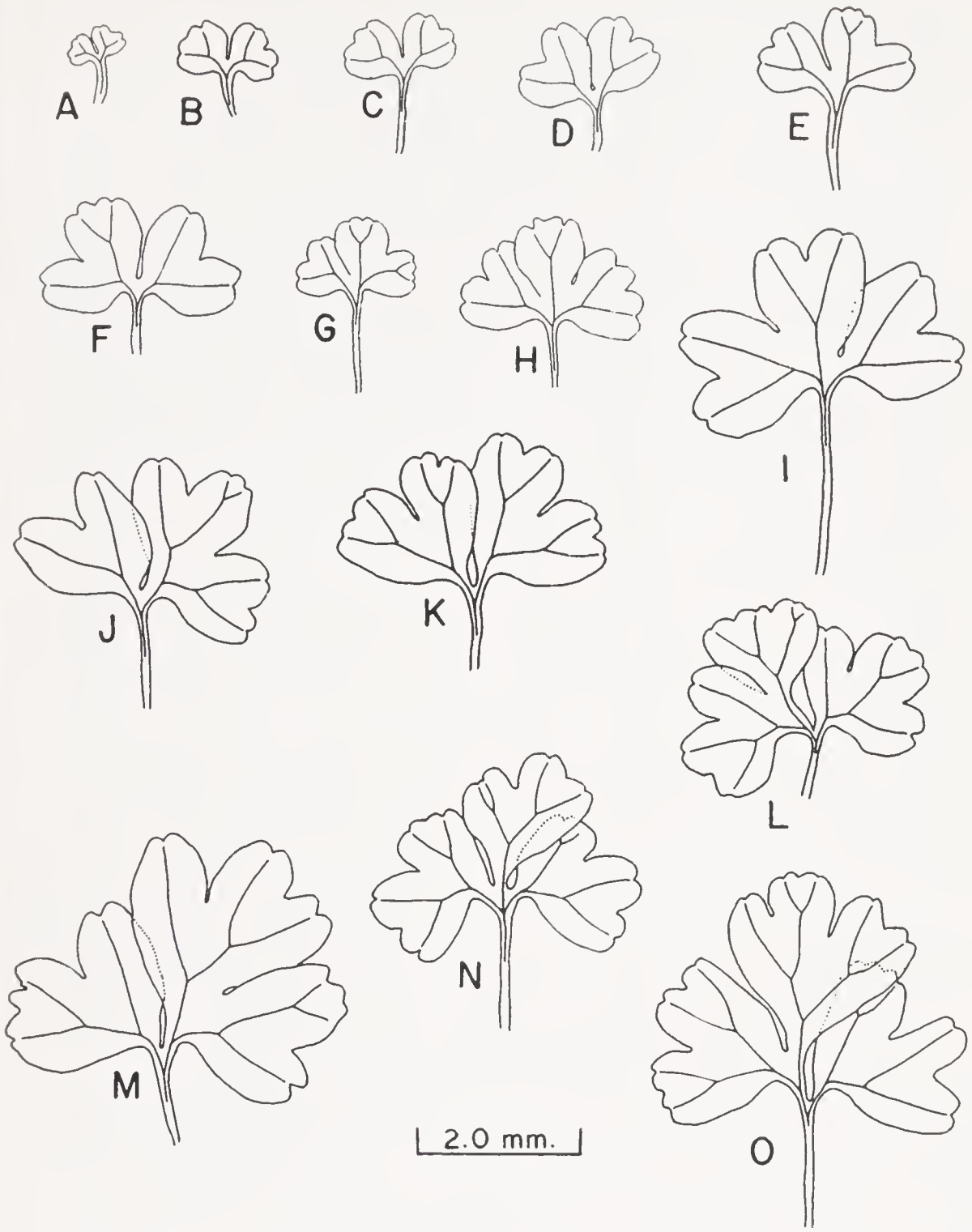

PLATE 18

HETEROBLASTIC SERIES OF SPOROPHYTE LEAVES IN *CYSTOPTERIS*

Fig. A-O. Leaves of young sporophyte of *C. bulbifera*.

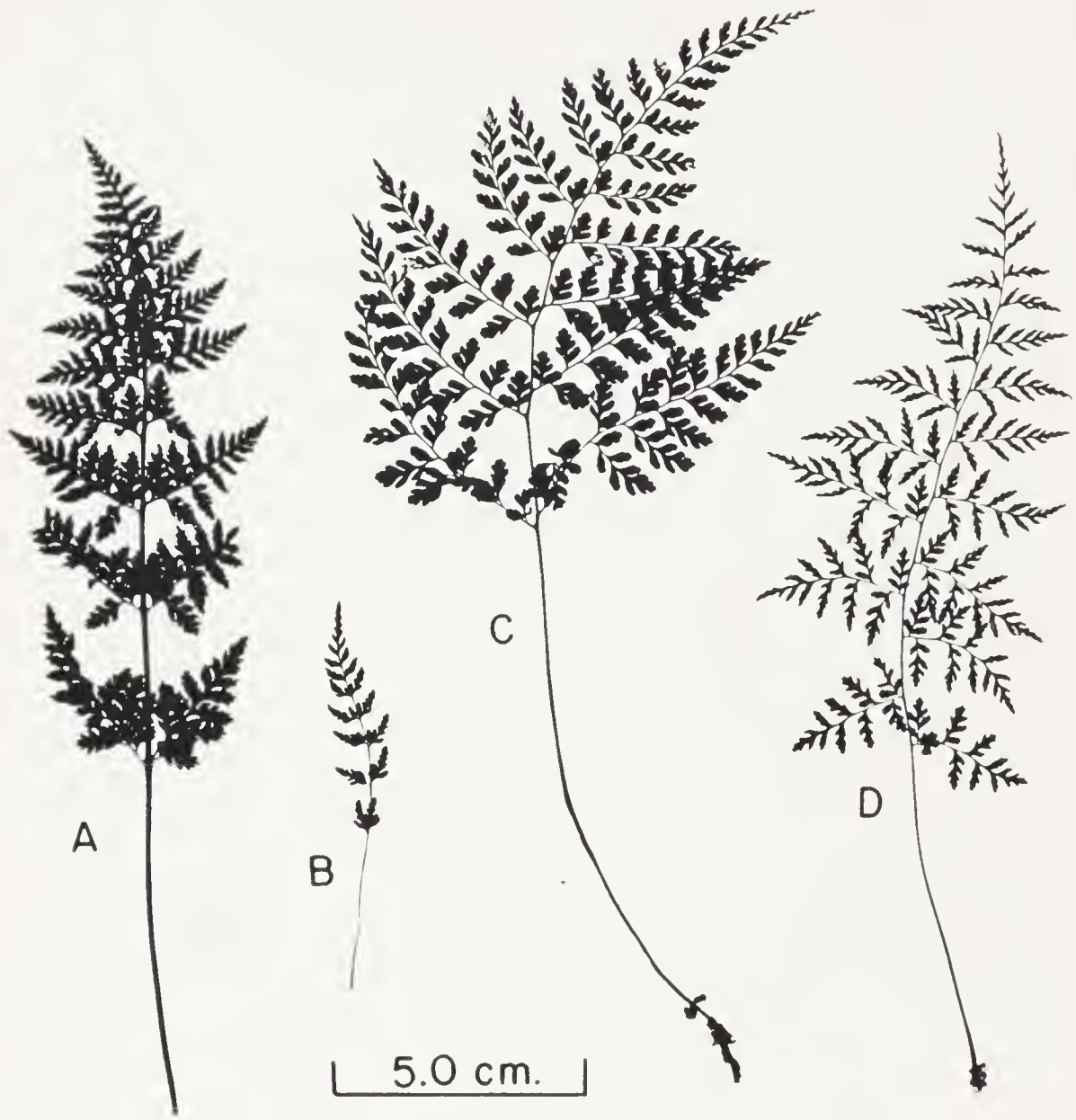

PLATE 19

SILHOUETTES OF MISCELLANEOUS *CYSTOPTERIS* TAXA

Fig. A. *C. fragilis* var. *apiiformis*. B. *C. X kansuana*. C. *C. sudetica* var. *moupinensis*. D. *C. fragilis* var. *huteri*.

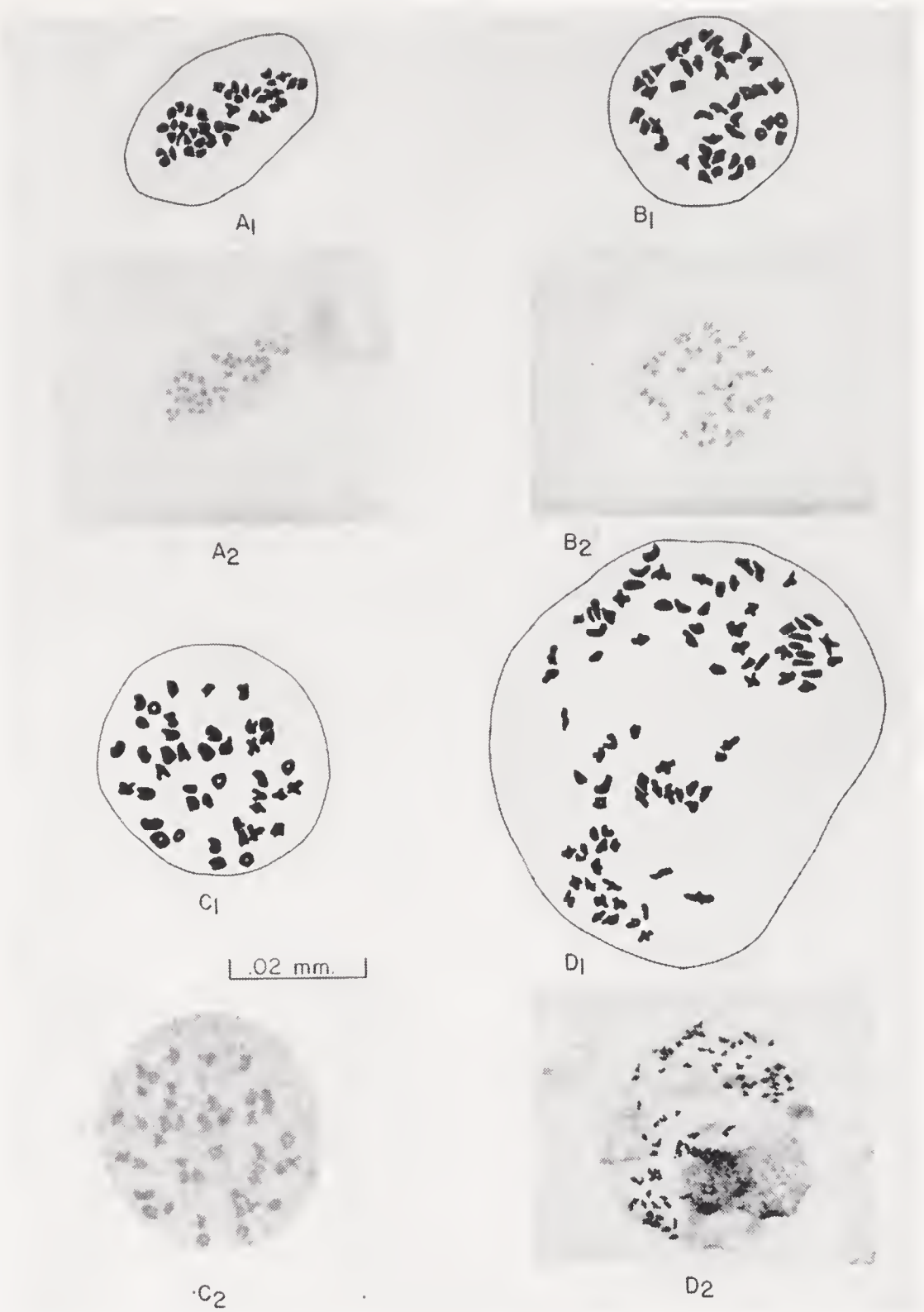

PLATE 20

CYTOLOGICAL SQUASHES IN *CYSTOPTERIS*

Fig. A. 1-2. *C. diaphana* X *protrusa* (Gold Hill, New Mexico, *Castetter* 9596. MICH.) $n = 42$. B. 1-2. *C. protrusa* (Elkmont, Tennessee, *Vannorsdall*, 30 Apr. 1956. MICH). $n = 42$. C. 1-2. *C. diaphana* (Santiago, Chile, *Valenzuela* et Vergara, 13 Oct. 1956. MICH). $n = 42$. D. 1-2. *C. fragilis* (Argentina, Provincia Neuquen, Parque Nacional de Nahual-Huapi, Peninsula Quetrihué, *Diem*, Aug. 1956. MICH). $n = 84$.

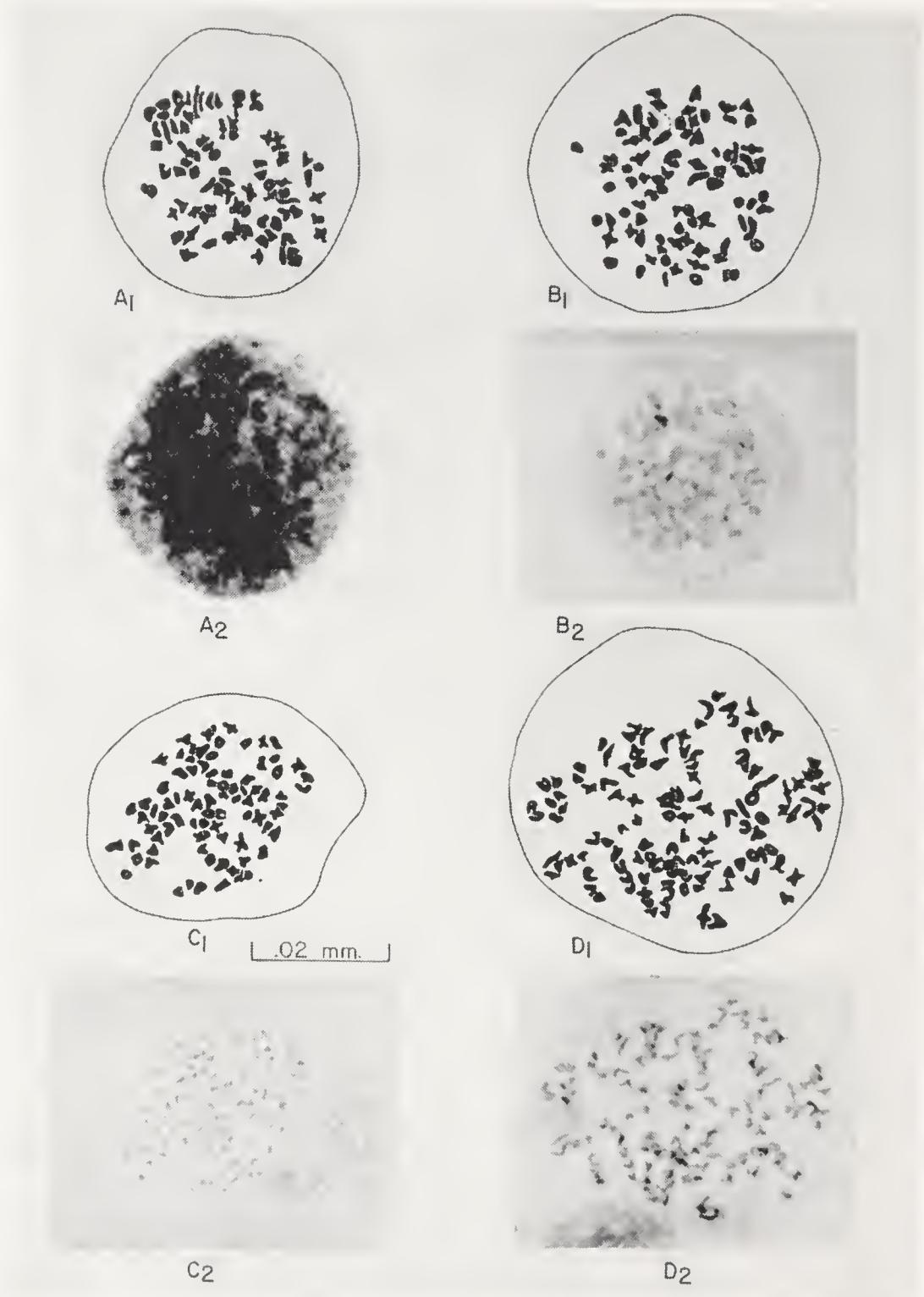

PLATE 21

CYTOLOGICAL SQUASHES IN *CYSTOPTERIS*

Fig. A. 1, 2. *C. fragilis* (Germany, *Merxmuller*. MICH). $n = 84$. B. 1, 2. *C. fragilis* (Yates Center, Woodson Co., Kansas, *McGregor*, MICH). $n = 84$. C. 1, 2. *C. X tennesseensis* (Clear Creek, Fairfield Co., Ohio. *Blasdell* 230 MICH). $n = 84$. D. 1, 2. *C. X laurentiana* (Ishpeming, Michigan, *Blasdell* 194 MICH). $n = 126$.

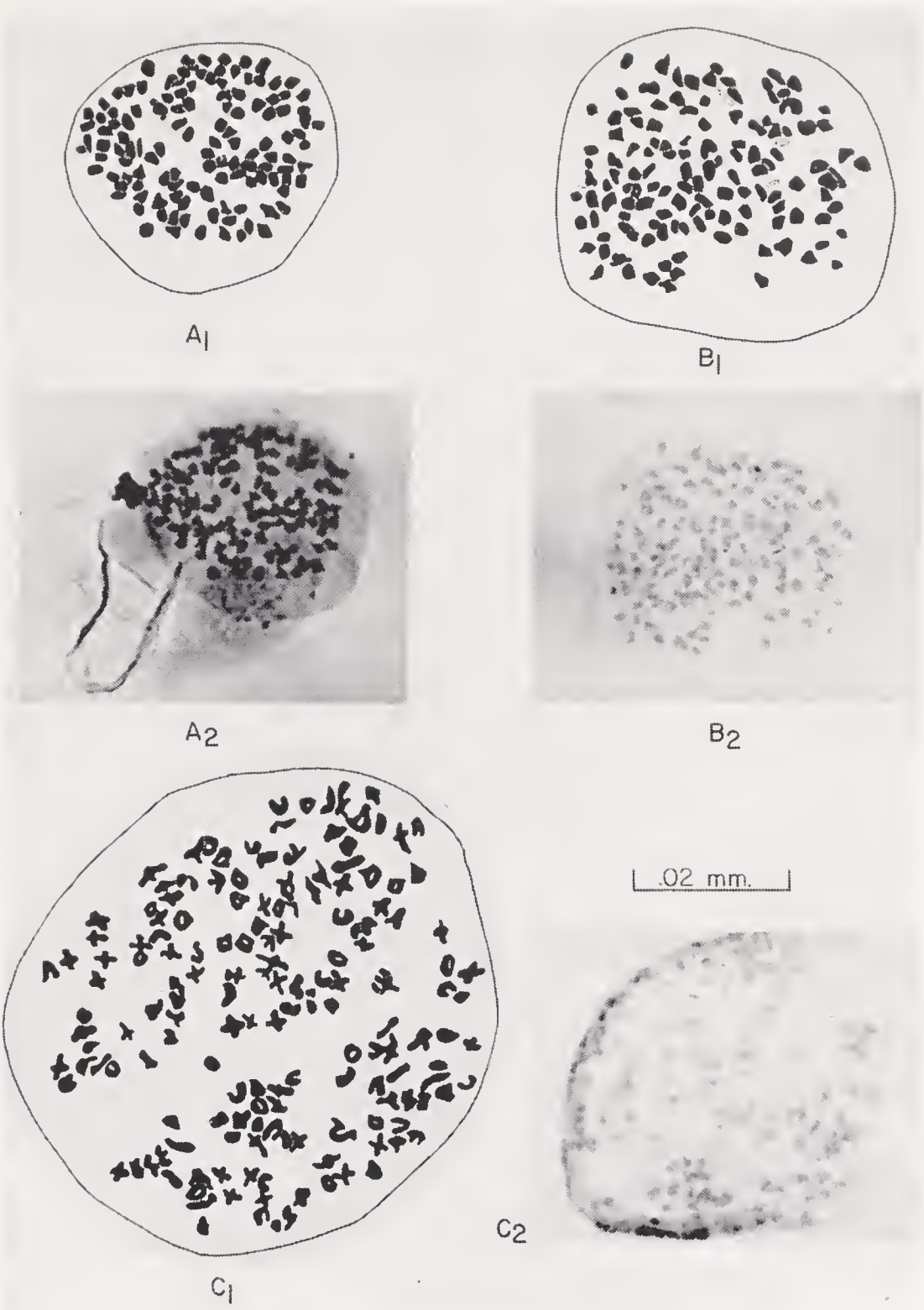

PLATE 22

CYTOLOGICAL SQUASHES IN *CYSTOPTERIS*

Fig. A. 1, 2. *C. fragilis* (Italy, *Ehrendorfer*. MICH). n = ca. 126. B. 1, 2. *C. diaphana* (Costa Rica, *Leon*, MICH). n = 126. C. 1, 2. *C. douglasii* (Mauna Kea, Hawaii, *Horner*. MICH). n = ca. 168.

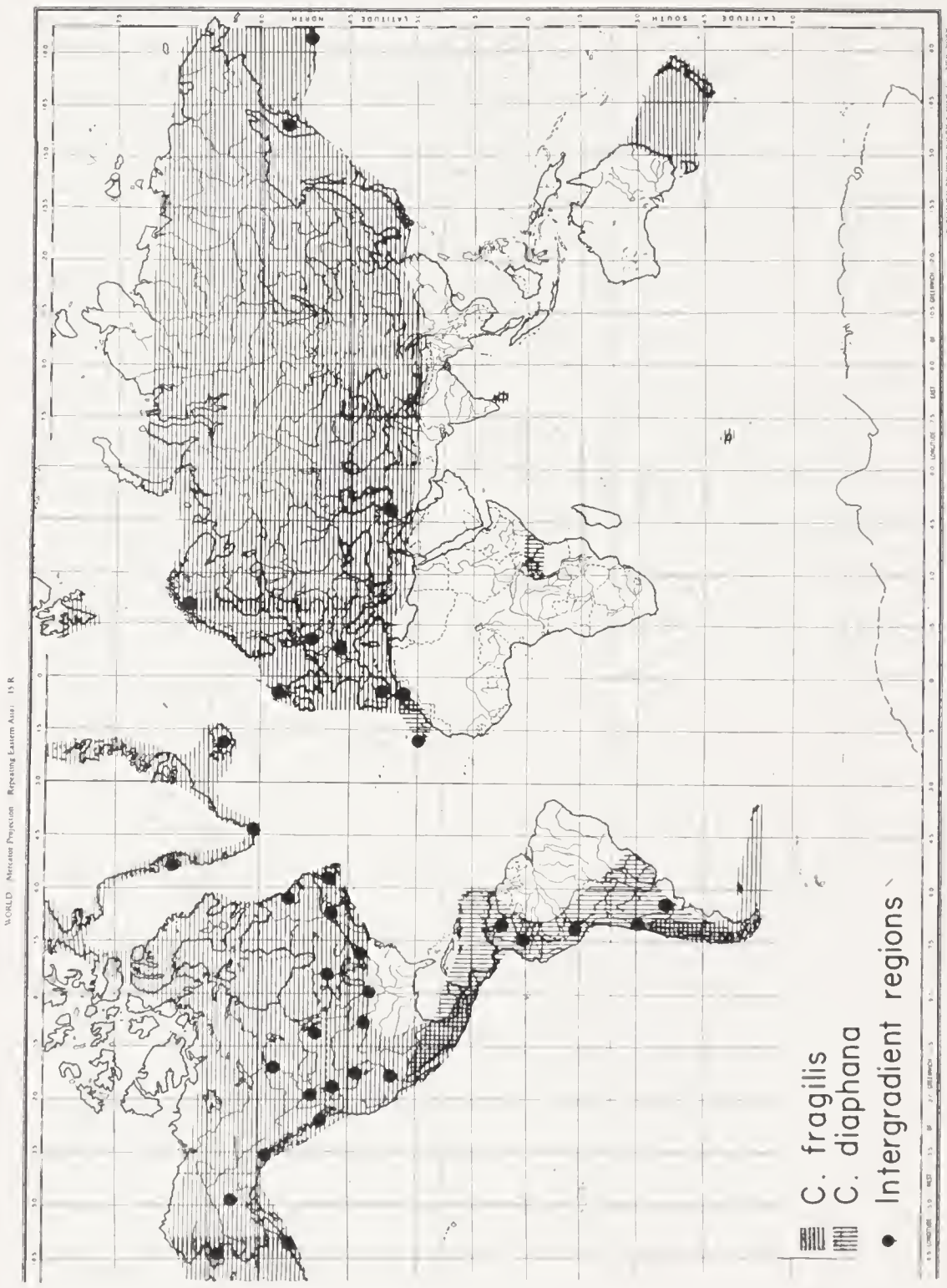

PLATE 23

DISTRIBUTION OF *CYSTOPTERIS FRAGILIS* AND *C. DIAPHANA*

THE BULLETIN OF THE TORREY BOTANICAL CLUB

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Memoirs
of
The Torrey Botanical Club

Vol. 21, No. 5 November 18, 1964

Editor
MURRAY F. BUELL

ORIGIN AND EVOLUTION OF FERNS

Papers presented at a symposium held at Corvallis, Oregon, under chairmanship of

THEODORE DELEVORYAS

Published for the Club by
THE SEEMAN PRINTERY
Durham, N. C.

Memoirs
of the
Torrey Botanical Club

Volume 21

Editor

Murray F. Buell

Manuscripts intended for the Memoirs should be sent to Dr. Murray F. Buell, Department of Botany, Rutgers University, New Brunswick, New Jersey.

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The origin and evolution of ferns

A Symposium Held At Corvallis, Oregon August 28, 1962

Sponsored by: Paleobotanical, General and Systematic Sections of the Botanical Society of America; American Society of Plant Taxonomists; American Fern Society; and Society for the Study of Evolution. In Conjunction with Meetings of the American Institute of Biological Sciences.[1]

Theodore Delevoryas
Editor

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[1] Publication of this symposium has been made possible by a grant (GN–259) from the National Science Foundation.

[2] An additional paper, "Protoxylem-metaxylem transition among the extant ferns," was presented by Professor David W. Bierhorst. This paper is not included with these; material included in that report has been incorporated in a paper published in 1960. (Bierhorst, D. W. 1960. Observations on tracheary elements. Phytomorphology 10:249-305.)

Introduction

Theodore Delevoryas

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A symposium such as this one on the "Origin and Evolution of Ferns" provides an ideal opportunity to review the current thinking on this perplexing problem. The ferns have been in existence for an incredibly long time, and are among the oldest known vascular plants in the fossil record. In fact, it is almost safe to say that of all the major groups of vascular plants in existence at the present time, more is known about the ferns in the fossil record than any other. In spite of their antiquity, and in spite of concentrated investigations on both fossil and extant forms, a number of problems of considerable importance remain. In general, we know about their origin from probably psilophytic ancestors; the particulars in this story are still missing, however. We know of the approximate time of appearance of the various groups in history; we are still unable to interrelate these groups, on the other hand. We are aware of their widespread distribution throughout the world at the present time; how they got to be where they are is still a mystery.

The problem of the origin and evolution of ferns clearly represents an example of the kind of problem that workers in diverse disciplines can attempt to solve by pooling their knowledge and working cooperatively. Paleobotanists specializing in Devonian rocks are best qualified to write about the beginnings of the group. Workers concentrating on Carboniferous plant fossils are in a position to indicate something about the perplexing fern-like plants that co-existed with the more nearly typical ferns. Subsequent evolution of new groups, many of them modern in aspect, is best treated by one familiar with Mesozoic and Tertiary floras. Among the modern ferns, attention must be paid to vascularization and patterns of specialization found there. Variation and possible evolutionary lines exhibited by the sporophyte generation, including attention to leaf morphology, may tell much about trends in the modifications of these structures in living ferns. Theoretical aspects and examination of the fern plant *in toto* may also be expected to present some new and provocative ideas.

All of these various avenues of research are represented by the contributors to this symposium. Other disciplines, as well, have much to

contribute; this symposium, on the other hand, has included only a representative cross section of all the branches of botany that have something to contribute.

In spite of progress made in each of the fields of endeavor, I am convinced that the ultimate solutions can come only by utilizing all information gained from all areas of research. Obviously the paleobotanist, even though eminently qualified to search out the possible beginnings of various fern lines, is not at all equipped to utilize cytological and genetic phenomena that must play an important role in determining certain critical aspects of fern evolution. The anatomist, although discovering fruitful concepts of tracheary specialization, realizes that one must consider the evolution of all parts of the plant, both gametophyte and sporophyte. Finally, one attempting to understand possible patterns of evolution based on theoretical considerations may succeed in obtaining various plausible schemes, but they can be valid only when verified by evidence from all disciplines. And in the end, any hypothesis must be tested by the fossil record.

This symposium, although not solving all problems concerned with the origin and evolution of ferns, indicates that great strides have been made along the various lines of investigation followed. A symposium such as this could not have been possible ten years ago. It is obvious that most of the significant advances reported in each of the papers have taken place very recently. It is encouraging, for that reason, to believe that within the next ten years we can expect similar strides, and that we will be much closer to understanding just what a fern is, where it came from, and how it got to be that way.

The Psilophytes and their relationship to the origin of ferns[1]

Francis M. Hueber

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Even at the beginning of a study of the Order Psilophytales, it is immediately obvious that the order represents a diverse group of plants. This diversity has grown in the years since the order was established by Kidston and Lang in 1917. One might say that the diversity had begun to develop even prior to that date. I am referring particularly at this time to some of the works of Sir J. W. Dawson whose genus *Psilophyton* became a receptacle for several plant forms, that is, plants of different morphology as well as those preserved only as fragments.

Psilophyton princeps was the source for the name of the order (Kidston and Lang, 1917), and Dawson's reconstruction of the plant (1872, 1888) has been reproduced again and again to illustrate the definition of a psilophyte. Yet, no organic connection was proved for the parts that were described and shown in the reconstruction. Solms-Laubach (1895) commented upon this fact but offered nothing in the form of a revision. However, Halle (1916) proposed that the fertile portions of the plant in the reconstruction be referred to a new genus and species: *Dawsonites arcuatus*, the specific epithet in allusion to the recurved, terminal sporangia. He also proposed that the type specimens of *P. princeps* be those described and illustrated by Dawson (1871) as *P. princeps* var. *ornatum*. The reconstruction, therefore, has been partly dismembered and cannot validly serve as an accurate representation of the species.

Perhaps in reality a symposium is meant to summarize relevant information up to the time of the meeting. However, as a means for emphasizing a point, I wish to present some new findings from research in progress on the genus *Psilophyton* and information on new specimens of plants to which I shall refer as cf. *Dawsonites arcuatus*.

During the field season of 1961 with the Geological Survey of Canada, collections of fossil plant remains were obtained from the Lower Devonian Sextant Formation on the Abitibi River in northern Ontario, Canada. The plant specimens are primarily compressions, however, some of the axes are preserved by pyrite. Among the plants that were collected are several

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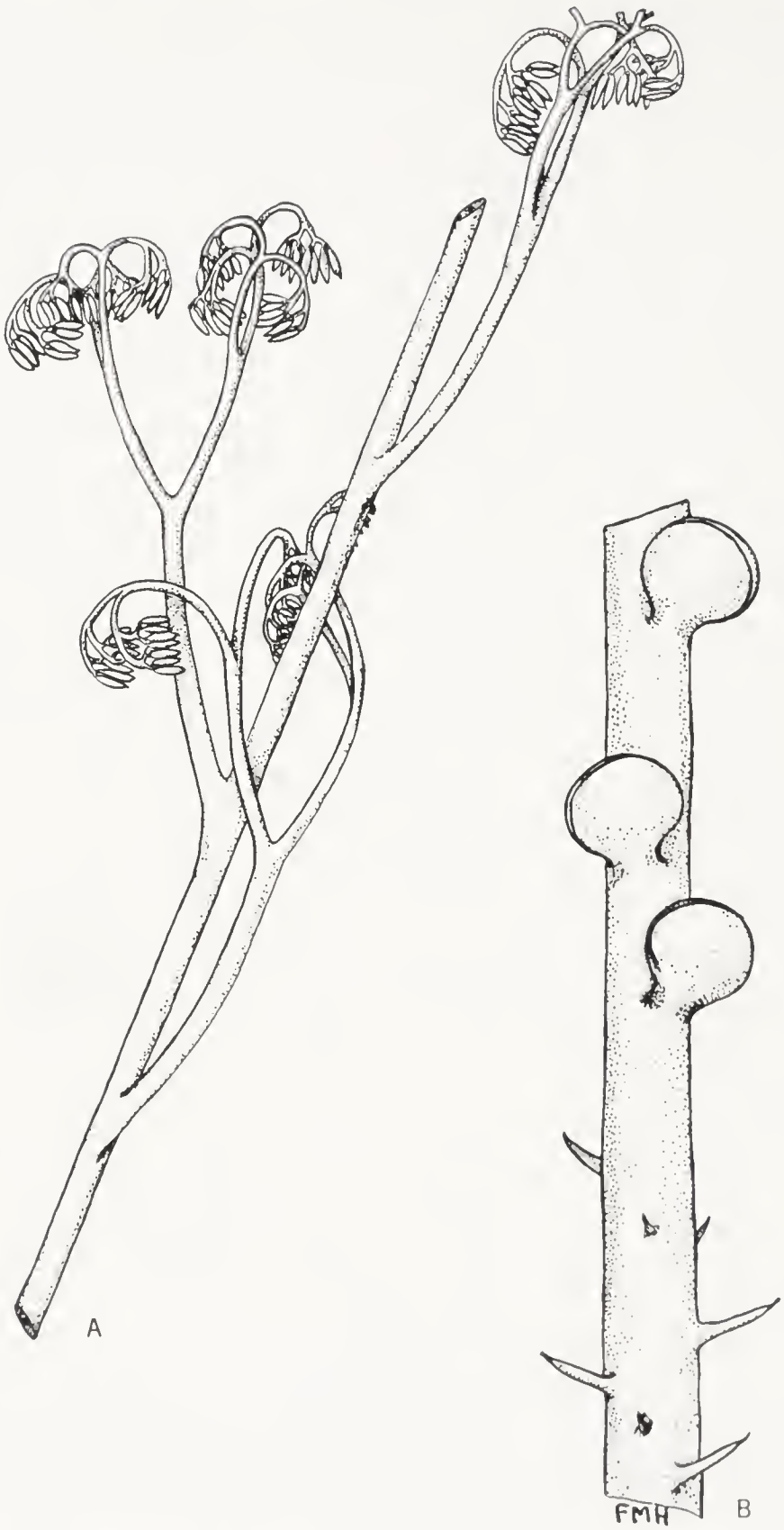

FIG. 1: A. cf. *Dawsonites arcuatus* Halle, reconstruction of axis with fertile branches bearing terminal sporangia. X 1. B. *Psilophyton princeps* Dawson, reconstruction of portion of fertile axis showing globose, lateral sporangia. X 5.

axes bearing clusters of terminal sporangia. Superficially these sporangium-bearing axes are referable to the species *Dawsonites arcuatus* and very closely resemble those illustrated by Dawson (1871, for *P. princeps*) and Halle (1916). However, careful picking away of the matrix from around the specimens revealed a much-branched structure bearing many sporangia (Fig. 1, A). The anatomy of the axis that supports the fertile branch system is rather simple. The xylem is primary, mesarch, and elliptical in cross-section. The region of the phloem and inner cortex is not preserved. Layers of an outer cortex composed of thick-walled cells and an epidermis are well preserved. A single, small, terete trace arises from one of the poles of the central xylem strand and passes off to the fertile branch system. Sporangia are fusiform and dehisce longitudinally. In transverse section, the sporangia are shown to have two layers, a thick outer one and a very thin inner one. The thin inner layer is a sac-like structure in which the spores are contained. Spores are very numerous and if they had been found isolated they would be included in the genus *Retusotriletes*. It is interesting to note at this point that Lang (1931) demonstrated a similar double-layered structure in the sporangia attributed by Dawson to *P. princeps*.

Though these new specimens are superficially referable to the psilophytes and to *Dawsonites arcuatus*, the reconstruction and this brief description serve to point out that the specimens are elaborately branched axes with anatomy that is generally interpreted as characteristic of the early "ferns."

In the use of the term "fern," the word is purposely set off by quotation marks and spelled with a small "f". Our knowledge is still limited as to the true nature of some members of the complex of plants in the early Devonian that seemed to have been leading toward eventual differentiation of the ferns.

In addition to the fertile axes described, several specimens of *Psilophyton princeps* were obtained at the Abitibi River locality. The hand specimens exhibit large numbers of spinous axes that in nearly every detail are identical to specimens obtained in Gaspé and in New York State (Hueber and Grierson, 1961). However, after maceration of the shale matrix with concentrated hydrofluoric acid as the solvent, several pieces of the axes were obtained that exhibit large, globose sporangia (Fig. 1, B). The cellular details of the epidermis of both the sterile and fertile axes are in total agreement with those details demonstrated by Edwards (1924) and Lang (1931, 1932) for the specific identification of *P. princeps*. Spines are much less numerous on the fertile axes than on the sterile material. The sporangia are borne on short, broad stalks and are arranged separately and randomly along the sides of the axis. A distal line of dehiscence

divides the sporangium in half, and when it is open along this line, the sporangium has a peculiar bivalvular appearance. Masses of spores have been found in some of the sporangia. The walls of the spores are unornamented; a trilete mark is present.

Croft and Lang (1942) illustrated very similar, if not identical, axes from the Lower Devonian Senni beds in Monmouthshire and Breconshire, Great Britain and referred to the material as cf. *Psilophyton princeps*. The authors were unable to prove conclusively the identity of their material, for no preparations could be made that would show sufficiently diagnostic characters for identification of the species.

Field work with the Geological Survey of Canada during the summer of 1962 yielded specimens of *P. princeps* from Dawson's type locality for *P. princeps* var. *ornatum* on Gaspé Bay (Dawson, 1871, p. 38). Several specimens were obtained that exhibit sporangia identical in form and arrangement with those from the Abitibi River site.

On the basis of this new information, *P. princeps* clearly does not belong with the typical psilophytes such as *Rhynia* and *Horneophyton*, but instead belongs in a different line of development within the group of plants presently referred to the Psilophytales.

Although any natural classification within the Psilophytales is premature, generally speaking there is increasing evidence in support of the concept of at least two main lines of development within the order as it is presently known. These two lines are based on the difference in the position of the sporangia; one line in which the sporangia are lateral on the axis and one line in which the sporangia are terminal. Some additional points of a general character may be added to indicate further differentiation between the two lines. These are: the sporangia in the terminal line are predominantly fusiform and exhibit longitudinal dehiscence; sporangia in the lateral line are predominantly globose or reniform and exhibit distal dehiscence. These differences in sporangial position, form and dehiscence are particularly obvious among the psilophytes of the Gaspésian Devonian floras with which my present research is concerned. I have introduced the new information on *P. princeps* and the axes referable to *Dawsonites arcuatus* from the Abitibi River locality as a means for emphasizing this apparent division in the Psilophytales.

Of the two divisions, the line with terminal sporangia comprises the greater variety of forms, differing in complexity of morphology and, where known, in anatomy. Complexly branching axes with terminal sporangia occur simultaneously with or earlier than the simple forms and it appears that many of these complex forms indicate differentiation toward the ferns

or even perhaps toward the pteridosperms. That they occur simultaneously with or earlier than the simple forms might indicate independent origins of the two, or longer geologic range for the simple forms; for either case we have no proof. If we are to trace the origins of the ferns among the psilophytes, in the broad sense, the line with terminal sporangia is apparently the most likely source.

In maintaining the concept of the Psilophytales, it is best not to visualize *Psilophyton princeps* as a typical psilophyte; instead, *Rhynia* should be held as the example. Because *Rhynia* is a simple plant in the group of plants exhibiting terminal sporangia, I do not infer or wish that my comments be interpreted to mean that *Rhynia* gave rise to the ferns. Some plant, pre-Devonian in age and of a structure similar to *Rhynia*, may have been the source. Any real proof for this is yet to be discovered and a more thorough study and evaluation of the Devonian floras of the world is required.

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Putative Devonian ferns

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A few introductory remarks will explain some of the limitations of our material and the choice of title. First, there are only rare cases in which a Devonian plant is known in its entirety. Many of our data are taken from fragments of plants, that is, individual organs or parts of organs. If the parent plants of these organs were known, the systematic affinities of the fragments might be shown to be quite different.

Two recent publications illustrate what I have in mind. The genus *Callixylon* has been recognized since 1911. It can be identified only by its anatomical structure and has been considered on that basis to be a gymnosperm. However, Beck (1960, 1962) has shown that it bore fern-like foliage and that its reproductive structures were those of a pteridophyte. It must, therefore, be removed from the gymnosperms. Incidentally, these data also suggest to me that anatomical structure is not so conservative as it is often held to be.

Similarly, *Pseudosporochnus* has been treated as an advanced, bushy psilophyte. Professor Leclercq of Liège and I (1962), on the basis of abundant and more complete material from Belgium, have shown that the plant was arborescent in form, bore ultimate appendages equivalent to fronds or leaves and, perhaps more important, had the anatomical structure of a cladoxylalean fern. Clearly it was no psilophyte.

In the same vein Walton (1957) showed that the Mississippian genus *Protopitys*, whose secondary xylem was gymnospermous, bore sporangia, possibly heterosporous, that had a pteridophytic appearance.

There is no gamble on my part if I predict that we shall continue to turn up evidence that requires such changes in classification. The work of Hueber (1962) on *Psilophyton* and on the fertile branches of *Dawsonites* that is presented in the preceding paper on this symposium is an obvious example.

Second, no matter how carefully the paleobotanist investigates the geological horizon whence his plants were collected, his data for the age of his plants may still be open to question for any one of several reasons that are beyond his control. This is particularly true of rocks that were laid down around the fringe of continental seas. These rocks lack the marine invertebrate fossils that serve as excellent indices of the age of

marine strata. They are, therefore, much more difficult to subdivide and to correlate than marine strata. They are also the source of some of our best fossil plants. When new evidence or a new approach leads the stratigraphic paleontologist to change the stratigraphic position of these "continental" strata, the paleobotanist is forced to change his conclusions accordingly. Thus, although one intends to attribute evolutionary or phylogenetic significance to data on Devonian plants by demonstrating that simpler forms preceded more complex ones, the exact knowledge of the age (stratigraphic position) of the horizon from which the plants were taken and an accurate analysis of the succession of floras at different localities is sometimes unavailable, sometimes incorrect.

The well-known assemblage of fossil vascular plants in Australia provides a good example of the result of a change in stratigraphic position. This flora is treated in most textbooks on paleobotany or morphology as the oldest known flora containing vascular plants and as Silurian in age. The age was determined chiefly by the species of graptolite of the genus *Monograptus* that is associated with the plants. However, Jaeger (1959) suggested that the species of *Monograptus* might be misidentified and that the plants might really be younger than Silurian. A subsequent paper (Jaeger, 1962) reports that the horizon in which the vascular plants occur is probably equivalent in age to the Lower Devonian of the Rhineland because the graptolites in the Australian beds are Devonian, not Silurian, species. A more complete account by Jaeger of the taxonomy of the graptolites involved still awaits publication. Nevertheless it looks as though conclusive evidence of vascular plants on the basis of macrofossils still points to the Silurian-Devonian boundary and not older Silurian as the time of first appearance of land plants. This could reduce materially the time interval during which evolution of early land plants could have proceeded. Time limitations preclude a discussion here of the inconclusive evidence provided by some less well-known supposed vascular plants older than Devonian and of the increasingly abundant literature on microfossils that might indicate an origin of vascular plants much earlier than Devonian time. (See Leclercq, 1956; Chaloner, 1960; Stewart, 1960; Obrhel, 1962; Roselt, 1962 for discussion of pre-Devonian fossils that may represent vascular plants and for two of the most recently described fossils that are presented as possible Silurian tracheophytes.)

In Lower Devonian strata we find representatives of Psilopsida, Lycopsida and probably Sphenopsida. Hueber has already introduced the next obvious question—are there ferns also in the Lower Devonian?—with his demonstration of the complex reproductive branch system of *Dawsonites*.

FIGS. 1-8: Fig. 1. *Protopteridium minutum* (From Arnold, after Halle). Fig. 2. *Trimerophyton robustium* (From Andrews, after Hopping). Fig. 3. Lower Devonian plant from Gaspé. a, outline of xylem strand and of outer cortex; protoxylem indicated by black line. b, cortex only partially preserved; xylem branched pseudomonopodially. c, d, e, show variation in configuration of xylem strand. Fig. 4. *Svalbardia polymorpha*. a, sterile. b, fertile (From Andrews). Fig. 5. *Archaeopteris* sp. a, sterile. b, fertile. Fig. 6. *Protopteridium*. a, sterile pinna. b, fertile pinna (From Eames, after Kräusel and Weyland). Fig. 7. *Aneurophyton* sp. a, fertile pinnule. b, portion of sterile frond. Fig. 8. *Reimannia aldenese*, outline of stem and of xylem. Protoxylem indicated in black, peripheral loop as a circle (After Arnold).

The following discussion outlines the kind of evidence available for the study of Devonian ferns, some anatomical and morphological characters that can be studied, and surveys a few Middle and Upper Devonian plants that are presumed to be "ferns."

The fossils are both flattened compressions and anatomically preserved petrifactions. Each type offers important evidence that would be greatly strengthened if it could be combined with the other to make a whole plant. Despite the discovery of occasional bits of petrified tissue in what is otherwise a compression, many of our Devonian plants are preserved in only one of these two ways. This additional incompleteness of Devonian fossils should be kept clearly in mind when evaluating the evidence on which hypotheses are based. It should serve also as a reminder that reports of older plants require substantial evidence if they are to be accepted.

In the Lower Devonian there is an interesting compression described by Halle from Central China as *Protopteridium minutum* (Fig. 1). It has flattened appendaged arranged in two rows. Some of them bear a slight resemblance to pinnules. Other appendages bear tufts of terminal sporangia. The resemblance to a frond of a fern is there despite our meagre information.

Another Lower Devonian compression is *Trimerophyton robustius* of Hopping (Fig. 2). This plant was originally included among specimens referred by Dawson to *Psilophyton*. Hopping (1956) has shown its branching to be much more complex than that of a psilophyte. Lateral branches are arranged spirally on a naked axis. Each lateral trifurcates immediately Each of the three branches produced trifurcates again, but unequally. The two smaller dichotomize twice producing four sporangial tips. The median branch dichotomizes three times and terminates in eight sporangia.

Trimerophyton, like *Dawsonites*, foreshadows the complex branching systems and masses of terminal sporangia that are found in younger strata and referred to the Coenopteridales. Both plants are more highly evolved than psilophytes of the *Rhynia* type yet lack any indication of true fronds. The pattern of branching of *Protopteridium minutum* is less complex but is more suggestive of fronds. Anatomy is so far unknown or undescribed in all three species.

It is easy to imagine that all three plants approach the archetype of ferns as proposed by Bower (1935, pp. 457-458). Bower conceived of a primitive type as having an upright shoot with radial symmetry and with very little differentiation between main axis and leaves. He proposed that leaves originated from lateral branches which forked dichotomously and

were not laminate and that a protostele characterized all parts of the axis. Associated with these vegetative characters he considered thick-walled, solitary, terminal sporangia to be the primitive type. Whether or not one wishes to follow all aspects of Bower's meticulously documented evolutionary series among ferns, it is clear that plants bearing features that he predicted are being found in Lower Devonian strata.

To continue the story of the Lower Devonian one step further I should like to mention an unpublished plant on which I am working (Fig. 3). It is a petrifaction rather than a compression. Two tissues are preserved in most specimens, the outer cortex and the xylem. The naked stems branch dichotomously and pseudomonopodially. The absence of appendages suggests that the plant is either a psilophyte or a primitive fern. The large size and the remarkable variation in the configuration of the xylem strand rule out the possibility of a close affinity to the psilophytes. In transverse section the xylem is terete, elliptical, triangular, 4-armed, or 5-armed. It is all primary with the possible exception of one stem. Xylem is mesarch and usually several protoxylem strands are present. Metaxylem tracheids are scalariform, with characteristic thin spots in the walls between the bars. Associated with the stems are masses of terminal sporangia with very thick walls and smooth spores bearing trilete scars.

This plant is more highly evolved than a simple psilophyte of the *Rhynia* type and some of its characteristics suggest the fern complex. Its branching pattern, the order of maturation of primary xylem, the arrangement of its protoxylem strands, the complexity of its stele, its possible massive terminal sporangia in large clusters all suggest affinity to ferns. However, at this stage it is difficult to say whether it points toward the group Coenopteridales, which is usually called fern, or toward the group Cladoxylales, which is perhaps fern, or, as some prefer to say, is a precursor of pteridosperms.

In summary, the earliest vascular plant flora, in the Lower Devonian, includes representatives, or at least precursors, of the 4 major subdivisions of Pteropsida. In making this point perhaps I should repeat that my omission of all reference to presumed vascular plants of greater antiquity is intentional.

The occurrence of four subdivisions in the Lower Devonian may have implications about the origin of land plants. Several hypotheses suggest themselves: a) the four groups evolved rapidly—within 15 million years (table 1)—perhaps from some simple psilophyte of the *Rhynia* type; b) land plants had a long pre-Devonian history that is not yet clearly elucidated; c) the four groups arose independently and more or less simul-

taneously from unknown ancestors, perhaps green algae. In the present state of our knowledge one cannot be dogmatic in supporting one possibility over the others. Despite ample speculation in the literature, I find no strong evidence in favor of a single hypothesis. The one undisputed fact is the existence of a wide variety of vascular plants in rocks of Lower Devonian age. If we achieve success in studies of the rate of evolution of vascular plants in Devonian time and if the time span occupied by the Devonian Period remains unchanged, the first hypothesis can be tested. Similarly the discovery of incontrovertible evidence of Cambrian or Ordovician vascular plants would support the second hypothesis. The third possibility will probably remain in the realm of morphological speculation, a likely course of events but hardly one we can prove with evidence as fragmentary as ours will always be. Obviously much work remains for the future.

TABLE 1. *Data for beginning and duration of subdivisions of the Devonian Period. See Kulp (1961) for brief discussion of the uncertainties with which these data are fraught and for the complete geologic column.*

Period	Unit	Began
Devonian	Upper	365 million years ago
	Middle	390 ± 5 million years ago
	Lower	405 + 10 million years ago

If precursors of ferns lived during Lower Devonian time, it is likely that they continued into the Middle Devonian. Again, however, we have the problem of knowing the internal structure of some species but not of others, of discovering radially symmetrical branch systems that can be interpreted as precursors of megaphylls but that do not look like typical leaves. Along with these difficulties we encounter some plants that seem to have evolved a fern-like leaf and, simultaneously, secondary wood that is reminiscent of gymnosperms. Two other morphological developments were common to several Middle and Upper Devonian plants. One is ultimate "pinnules" that were nothing more than dichotomously forked, often recurved, ultimate branchlets (Fig. 7) borne on a lateral branch system that may have been either three-dimensional or flattened, and that seems to have been homologous to a leaf. The other is the production of clusters of sporangia on ultimate branchlets that were recurved or incurved (Fig. 7). The sporangia were terminal on short stalks. These characters are combined in various ways in the several genera. As a result, the grouping of

genera into families and orders is more a matter of convenience than of proven natural affinity. The classification used below is only one of several that have been suggested and should be regarded only as tentative.

The Protopteridales (Zimmermann, 1938; Høeg, 1942) has been used by some authors to include a few of the better-known genera that have some morphological characters of ferns. *Svalbardia* (Høeg, 1942) was at least a foot and a half, perhaps 6 feet, in height, and possessed a main stem and lateral branches that were approximately opposite or possibly whorled in arrangement (Fig. 4). On the lateral branches, ultimate ramifications consisted of non-laminate, dichotomously forked branchlets. These ultimate branchlets may represent the equivalent of pinnules. Fertile branches bore sub-opposite, filiform, lateral divisions on the upper side of which the sporangia were borne on short stalks. The branching and the mode of bearing sporangia, along with the occasional tendency for sterile appendages to be webbed, suggested originally that *Svalbardia* was an immediate ancestor of *Archaeopteris* (Fig. 5). It was assumed that extensive webbing of the ultimate branchlets would have produced pinnules of the *Archaeopteris* type. The discovery by Beck that *Archaeopteris* was borne on the gymnospermous axis *Callixylon* seems to remove *Archaeopteris* from any connection with Protopteridales and to negate the satisfying hypothesis that *Svalbardia* was its ancestor. Nevertheless *Svalbardia* does show what the ancestral condition of *Archaeopteris* might have been morphologically. If the anatomy of *Svalbardia* is ever discovered, perhaps the two will prove to be more closely related than seems now to be the case.

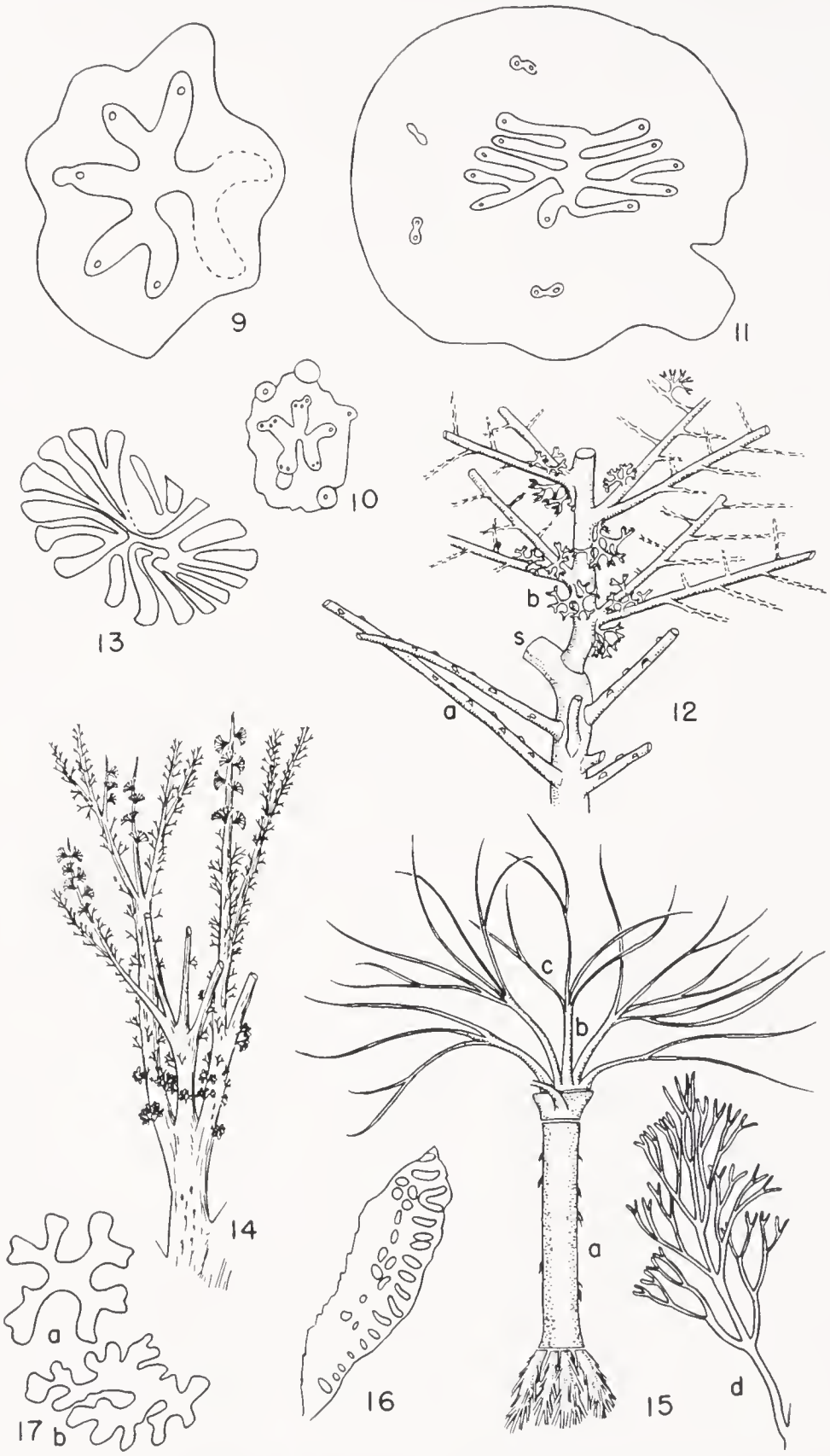
Somewhat more fern-like than *Svalbardia* is the genus *Protopteridium* (Fig. 6). Its branching axes produced some laterals that simply dichotomized as in a psilophyte, others that were more contracted, flattened and pinnule-like. Still others were recurved and bear rows of sporangia that were terminal on minor divisions on the concave, inner surface. Kräusel and Weyland (1938) described the wood of *Protopteridium* as a three-lobed primary xylem strand surrounded by abundant secondary xylem. The latter was composed of tracheids, some with scalariform pitting and some with several rows of pits. Uniseriate vascular rays were also present. It is quite apparent from the morphology of *Protopteridium* why several authors have suggested that it, more than any other genus, illustrates the origin of megaphylls from the naked branching system of the Psilopsida.

Aneurophyton (Fig. 7) had some of the characters seen in *Svalbardia* and *Protopteridium*. It may have been a large plant with a trunk and large lateral branches, perhaps two feet or more in length, that seem to be homologous with leaves or fronds. The lateral branches were three-dimen-

sional despite the fact that they are usually illustrated as though flattened into one plane like the leaves of most modern ferns. Anatomically the frond was characterized by a triangular protostele surrounded by gymnospermous secondary xylem. The xylem was mesarch and some sections indicate that numerous strands of protoxylem were present rather than the three that are expected on the basis of the triangular shape of the primary xylem. This configuration was repeated in all divisions of the frond except in the ultimate "pinnules" that were without vascular tissue. Sporangia were borne in clusters on incurved ultimate pinnules.

Tetraxylopteris Beck (1957) shared some of the characteristics of *Aneurophyton* such as three-dimensional branching systems with recurved ultimate pinnules, large clusters of sporangia of one kind, a protostele with numerous protoxylem strands and gymnospermous secondary xylem. It will be described further by Beck in the next paper.

In the Protopteridales one sees only slight differentiation between stem and leaves, leaves that still resemble branch systems in their three-dimensional pattern and their lack of laminae. Even the leaves that are flattened and more frond-like are easily recognizable as slightly modified branches. Sporangia are terminal and in clusters. Anatomy where known shows a mesarch protostele with numerous protoxylem strands and secondary xylem composed of tracheids with multiseriate bordered pits and narrow, high vascular rays. It is particularly interesting to note the relative complexity of the wood in relation to the simplicity of the external morphology. This intriguing combination of characters shows immediately the reason for uncertainty as to whether or not all of these plants are ferns. Their mode of reproduction, their tendency to produce fern-like leaves, and their mesarch xylem with numerous protoxylem strands point toward ferns, but their secondary xylem seems to indicate otherwise. It is possible that many of the Protopteridales are precursors of pteridosperms. The forked ultimate pinnules of *Aneurophyton* and *Tetraxylopteris* are similar to those of *Sphenopteris olivensis* Stockmans (1948) and *Diplotmema pseudokeilhaui* Stockmans (1948). The latter two are much closer to pteridosperms on the basis of their resemblance to Carboniferous species, although no seeds have been found to prove this point. Parallel to this development is the presence of somewhat similar pinnules on the coenopterid fern *Rhacophyton*. Evidently as the megaphyll evolved in several groups, the pinnules passed through similar stages. For further discussion of the problem of the fern type of leaf see Nemejc (1950). Obviously much more information about the members of the Protopteridales, and also related groups, is required before we can prove whether or not they are ferns and whether they



FIGS. 9-17: Fig. 9. *Arachnoxylon kopfi*, outline of stem and of xylem. Peripheral loops indicated by circles. Fig. 10. *Iridopteris eriensis*, outline of stem, some append-

are precursors of fern groups, pteridosperms, or some other group. One conclusion, however, seems amply justified. This is that external morphology, mode of reproduction and anatomical structure were evolving at different rates and in different directions. The result is plants that do not fit readily into our systems of classification which are based on plants whose life history is understood more completely. Nemejc (1960) provides an example with his new group, Psygmophyllopsida. He erects this group for plants whose characters fit more than one subdivision of tracheophytes. They show relationships to Lycopsida, Sphenopsida and to the Carboniferous group Noeggerathiineae. From this line he suggests that several gymnospermous groups have been derived.

A second order that includes ferns of Devonian age is the Coenopteridales, most of whose representatives are found in Carboniferous strata. Three genera, *Reimannia*, *Arachnoxylon*, and *Iridopteris* have been described by Arnold (1935, 1940) and Read (1938) from Middle Devonian strata. I have found the first two genera in the Upper Devonian as well. All are preserved only as petrifactions of short axes less than 3 cm. long and under 1 cm. in diameter. The three (Figs. 8, 9, 10) possessed variously lobed protosteles surrounded by cortex. Traces to appendages were pinched off the tips of the xylem arms, but the appendages were not preserved. The xylem is mesarch and protoxylem areas are located near the tips of the arms of xylem. Protoxylem is usually accompanied by a lacuna, called a "peripheral loop," that results from the breakdown of parenchyma-like cells and some protoxylem cells.

For these plants Arnold (1940) erected the suborder Iridopteridineae of the Coenopteridales. He considered them to be intermediate between psilophytes and true coenopterids. The mesarch primary xylem, the peripheral loops and the pinching off of the traces to appendages are the characters that are most fern-like. Anatomically there is little evidence of relationship between these plants and the Protopteridales which had already evolved cambial activity. Whereas the Protopteridales display morpho-

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ages, and xylem; both larger and smaller appendages are produced; peripheral loops indicated by circles (After Arnold). Fig. 11. *Asteropteris noveboracensis*, outline of stem and of xylem; clepsydroid traces shown in cortex, with peripheral loops (From Hueber). Fig. 12. Rhacophyton zygopteroides, stem(s) with sterile (a) and fertile (b) fronds (Modified from Leclercq). Fig. 13. *Cladoxylon dawsoni*, outline of xylem only. Fig. 14. *Cladoxylon scoparium*, habit and sterile and fertile appendages. (Modified from Kräusel and Weyland). Fig. 15. *Pseudosporochnus nodosus*, a. stem, b. branch of first order, c. branch of second order, d. single frond from branch of first or second order. (Modified from Leclercq and Banks). Fig. 16. *Xenocladia medullosina*, outline of portion of stem with peripheral, radially aligned strands of xylem and central, circular strands. Fig. 17. *Schizopodium davidii*, outline of a single xylem strand (a) and a more complex strand (b). (From Hueber).

logical features of a fern precursor, these plants display anatomical characters that might be expected in the precursors of ferns.

A fossil that has been widely accepted as the oldest representative of coenopterids is the genus *Asteropteris* (Fig. 11). It, too, is known only as a petrifaction, and Dawson's original single specimen seems to have been lost. Hueber (1959) has rediscovered the genus in the Upper Devonian of eastern New York and another specimen indicates its presence in Middle Devonian deposits as well. Its xylem was deeply lobed into 10-14 arms, each of which shows a peripheral loop near its extremity. Traces were pinched off the tips of the arms in spiral order but are preserved only within the wide cortex. Further out in the cortex the traces became bilaterally symmetrical, elongate-elliptic in cross section (clepsydroid) with one protoxylem strand at each extremity and, finally, they show two protoxylem strands at each extremity. No actual appendages are preserved.

Petrified fragments of other axes are abundant in Middle and Upper Devonian in New York State. They too suggest the presence of ferns on the basis of characters similar to those already described. Their fragmentary condition however prevents them from adding significantly to our accumulated knowledge.

In Upper Devonian time there occurred the genus *Rhacophyton* (Fig. 12) that Leclercq (1951, 1954) has reconstructed so beautifully. A stout axis (stem) bore sterile fronds which gave rise to two rows of pinnae, each of which bore two rows of pinnules. The latter possessed no lamina but dichotomized several times. The fertile frond bore two rows of pinnae. However each pinna forked immediately after leaving the axis so that the frond seems to have borne four rows of pinnae as in zygopterid ferns of the Coenopteridales. Pinnae bore two rows of secondary pinnae which in turn bore ultimate pinnules like those of the vegetative pinnae. In the upper parts of the fertile frond two dichotomizing branch systems hung down close to the origin of the pairs of pinnae. These terminated in sporangia. The plant is treated by Leclercq as a member of the Zygopteroideae that combines the characters of two families, the Clepsydraceae and the Etapteridaceae. The preservation in *Rhacophyton* of both anatomical structure and external morphology makes it the most complete coenopterid yet found in Devonian strata.

A third group of organisms appeared as early as the Middle Devonian and continued on up into Carboniferous time. Whether or not these, the Cladoxylales, were true ferns, they do show several characters found among the ferns. The Devonian representative that is most characteristic of the

genus is *Cladoxylon dawsoni* (Read, 1935). It is preserved as a short axis, petrified in calcium carbonate, from Upper Devonian deposits in central New York. The illustration (Fig. 13) is drawn from the type block at the New York State Museum, and it shows the numerous, radiating xylem strands each with a peripheral loop around which protoxylem is located. Mississippian representatives, upon which the genus was founded, show traces to appendages arising from the extremities of several of the arms of xylem, several strands entering each appendage. Unfortunately neither traces nor appendages are preserved on this Devonian representative.

Kränsel and Weyland (1926) described the morphology of a compression specimen from the Middle Devonian of Germany under the name *Cladoxylon scoparium* (Fig. 14). They placed the plants in *Cladoxylon* because small portions of the stele were preserved, and they show the much dissected pattern of typical members of the genus, all of which are known only as petrifactions. Some authors have indicated that Kräusel and Weyland's specimens should not be designated as *Cladoxylon* because the name was instituted for petrifactions whereas their plants possess external morphology as well as anatomy. *Cladoxylon scoparium* had a much branched axis bearing small, bifurcated sterile "pinnules" and fan-shaped groups of appendages that were terminated by sporangia.

Leclercq and Banks (1962) have restudied the Middle Devonian genus *Pseudosporochnus* (Fig. 15) and shown that it, too, has the anatomical structure of a cladoxylalean plant. Externally it was characterized by a large axis terminated by a crown of branches. The latter ended in another crown of branches, some of which may have dichotomized. Ultimate appendages (fronds) were borne spirally on the second order branches, probably originally on all branches. The leaves possessed a main axis that gave rise to a pair of laterals two or more times. Each of the laterals underwent three dichotomies to terminate in 8 tips. The central axis similarly terminated in dichotomies. Some of the leaves were fertile, and each tip was terminated by a pair of sporangia. Anatomically the dissected xylem strand is found in the roots and in branches of the first and second order. The leaves appear to have had a single strand of xylem probably in the form of a clepsydroid trace like that in *Rhacophyton*. Such a fundamental difference in anatomical structure between branches and ultimate appendages leads to the interpretation that these appendages can be regarded as leaves. The fact that the appendages are flattened in one plane rather than being three dimensional substantiates the interpretation. Exactly how this situation compares to *Cladoxylon scoparium* will

not be known until the vascular supply to the appendages of the latter is discovered. However the general similarity of the two plants in gross morphology and stem anatomy suggests that the ultimate appendages of *C. scoparium* may also be leaves (fronds). This new interpretation of *Pseudosporochnus* as a cladoxylalean rather than as an advanced psilophyte tends also to confirm Kräusel and Weyland's interpretation of *Cladoxylon scoparium*.

Two other plants found in Middle and Upper Devonian deposits in New York have been placed in the Cladoxylales—*Xenocladia medullosina* Arnold (1952) and *Schizopodium* Harris (Hueber, 1959). Both plants are known only as pieces of petrified axes, the former 5 cm. or more in diameter, 10 cm. in length and the latter 4-8 mm. in diameter and up to 13.5 cm. in length. *Xenocladia* (Fig. 16) is characterized by numerous central, circular steles that are composed almost exclusively of secondary xylem. These are surrounded by a band of radially aligned, elliptical steles. The latter consist of both primary and secondary xylem and walls of the tracheids have one to four rows of bordered pits. It is the number and arrangement of the steles that requires assignment of *Xenocladia* to Cladoxylales. Little else is known about this plant. *Schizopodium* (Fig. 17) is less obviously cladoxylalean. It had a central protostele whose simplest pattern is four arms in the form of a cross, with each of the arms lobed once or twice at its extremity. In some specimens the lobing of the xylem is very complex and portions of the strand are completely detached from the main mass of xylem. This situation has led to the interpretation that *Schizopodium* is mid-way between psilophyte ancestors and cladoxylaleans that have numerous steles. Primary xylem is exarch; tracheids of the metaxylem are covered by multiseriate bordered pits. Certain arms of the xylem are surrounded at their extremity by radially aligned cells that simulate secondary xylem or that may represent only regular divisions in a procambial strand. The type of "secondary" xylem produced in this way is very similar to that seen in typical members of the cladoxylales. No appendages or traces to appendages are known in either *Xenocladia* or *Schizopodium*.

The Cladoxylales, then, are plants that ranged from Middle Devonian into Mississippian time, possibly somewhat longer. All except *Cladoxylon scoparium* and *Pseudosporochnus* are known only by their anatomical structure which is characterized by several to many strands of xylem ("steles"). Individual strands in transverse section are circular, elliptical, or variously bent or forked. Appendages in the Mississippian species are supplied by several bundles. In some species the bundles to appendages

are elongate-elliptical in cross section, with protoxylem areas at each end (elepsydroid). Peripheral loops are present in many species and secondary xylem varies from sparse to abundant around each lobe or plate of xylem. The group shares with the Coenopteridales the peripheral loops and flattened (elepsydroid) leaf traces. Its numerous xylem strands and secondary xylem forecast the seed fern complex and its numerous terminal sporangia (known only for two species) recall the psilophytes and are shared with the Coenopteridales and Protopteridales.

Earlier I mentioned that the production of dichotomized, recurved ultimate appendages on branch systems that are homologous to fronds is a character that is repeated persistently once it appears. Several genera of Middle and Upper Devonian age in the order Protopteridales display this character. It appears also in the Coenopteridales, in *Rhacophyton*. Similar pinnules appear in fronds of Carboniferous aspect that occur in the highest (youngest) Devonian strata in Belgium, for example in *Diplotmema pseudokeilhaui* and *Sphenopteris olnensis* (Stockmans, 1948). Whether these plants are ferns or seed ferns is not yet certain. Nevertheless they may be a product of evolution of the protopteridalean line, and they form a close link between Devonian and Mississippian floras.

In conclusion several points are worthy of emphasis.

1. It appears that plants assignable to a generalized fern complex appeared in the Lower Devonian along with psilopsids, lycopsids, and sphenopsids.

2. By the Middle Devonian at least three groups of plants with fern-like characters are present, Protopteridales, Coenopteridales and Cladoxylales. There is no assurance that these three groups are mutually exclusive nor that they are the only fern-like groups present in the Devonian.

3. Evidence from anatomy suggests that the Protopteridales may have evolved in the direction of seed ferns and the arborescent habit.

4. The Cladoxylales demonstrate characters of both psilopsids and zygopterid ferns. Anatomically they foreshadow the medullosan seed ferns. The group as a whole seems to have become extinct rapidly.

5. The Coenopteridales are a large and diverse group, some of which may have given rise to true ferns, and some of which are doubtless evolutionary blind alleys.

6. Of the three orders named, the Protopteridales impress me as being the least, and Coenopteridales the most, like true ferns. Cladoxylales occupy an intermediate position. Evolution was proceeding in several directions during Devonian time and fixed types had not yet been produced

as is shown by the difficulty in classifying the fossils that are found. Pichi-Sermolli (1959, p. 453), for example, excludes Cladoxylopsida and the genera here included in the Protopteridales from his phylum of ferns, the Filicopsida.

7. Some of the characters possessed by early fern-like plants are:
   a) lateral branch systems resemble leaves, at first three dimensional, later flattened in one plane.
   b) leaves at first non-laminate; pinnules repeatedly divided.
   c) xylem strand lobed to extremely dissected, pith absent.
   d) primary xylem mesarch.
   e) protoxylem strands often numerous.
   f) peripheral loops often accompany protoxylem.
   g) pseudo—or true secondary xylem (least common in Coenopteridales).
   h) pitting often circular bordered and multiseriate.
   i) sporangia, where known, massive and terminal.

8. It is quite possible that some, or many, of the characters listed were shared by early ferns and precursors of pteridosperms.

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The woody, fern-like trees of the Devonian[1]

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The Devonian has been often described as a period of sparse, low vegetation. Even the Upper Devonian is pictured as having few, scattered, relatively small trees, but there is now good evidence, and more accumulating constantly, that there were extensive, dense forests of large trees during Upper Devonian times. We know that there were at least 3 genera of woody, fern-like trees in the Devonian, and these are probably represented by 5 organ genera: *Aneurophyton*, *Eospermatopteris*, *Tetraxylopteris*, *Archaeopteris* and *Callixylon*. *Aneurophyton* is the oldest, occurring first in the early Middle Devonian, and extending into the Upper Devonian. The others are known only from Upper Devonian beds, except *Callixylon* which is common in the Upper New Albany shale which seems to be of Lower Mississippian age.

The three genera which we shall consider are *Aneurophyton*, the probable stem and stump casts of which are named *Eospermatopteris; Tetraxylopteris*, of which we know only the foliage and small stems; and *Archaeopteris*, the structurally preserved stems, roots and secondary wood of which are called *Callixylon*. We are confronted with three questions regarding the significance of these genera to the origin and evolution of ferns.

1. Do these plants represent a primitive fern stock or direct ancestors of the ferns?

2. If they are neither fern ancestors nor primitive ferns, with what groups do they show the closest phylogenetic relationship?

3. Have they given rise to any major groups of plants?

Before these questions can be answered we must examine in some detail the morphology and anatomy of each genus.

Aneurophyton-Eospermatopteris—*Aneurophyton* was described initially by Kräusel and Weyland in 1923 from the Devonian of Elberfeld, Germany. The plant did not possess typical, laminate leaves, but instead, frond-like branch systems which apparently functioned as leaves. These branch systems were terminated by once or twice-forked, recurved, ultimate segments. Some parts of fertile branch systems were terminated by clusters of sporangia that replaced the terminal dichotomous systems of the vegetative fronds. These branch systems were at first thought to be bilaterally symmetrical,

[1] Supported in part by National Science Foundation Grant 13223.

but when Kräusel and Weyland (1929) found that a 3-angled primary xylem strand was repeated in all parts of the system, they suggested that the branch system was probably radially symmetrical. A similar opinion has been expressed more recently by Arnold (1940) and Leclercq (1940). In addition to the absence of laminae, the repetition of structure further suggests that the frond-like structures are indeed branch systems.

The secondary xylem has been called gymnospermous, and is characterized by tall rays, and tracheids with hexagonal bordered pits on both radial and tangential walls.

In 1924 Goldring described a genus of supposed seed ferns from Gilboa, New York. For these plants she established the genus, *Eospermatopteris*, and included in it vegetative foliage (Fig. 14), apparently identical with that of *Aneurophyton* (which was unknown to her at the time); structures which she considered to be seeds; microsporangia, although not attached to the foliage; and, finally, large stumps preserved as sandstone casts with which the foliage was associated, but not in organic connection. Subsequently Kräusel and Weyland (1935) discovered, in association with *Aneurophyton*, stem fragments with surface marking identical to those of *Eospermatopteris* stumps. They also isolated spores from the supposed seeds of *Eospermatopteris*.

It seems probable, therefore, that *Aneurophyton* and *Eospermatopteris* are two names which have been applied to the same plant, and it is clear that there is no evidence that it was a seed plant. Although the stumps and stem fragments have not been found in organic connection with foliage, it is likely, because of their association in the same beds in two different localities, that these organs represent parts of the same plant. They are now considered as organ genera, the name *Aneurophyton* being applied to the foliage, and *Eospermatopteris* being applied to the stumps and stems. Goldring's reconstruction is shown in figure 14.

Tetraxylopteris—This plant (Beck, 1957), from the Upper Devonian of New York, is similar in many ways to *Aneurophyton*. Like *Aneurophyton* it is characterized by radially symmetrical, leaf-like branch systems terminated by recurved ultimate segments (Fig. 1). Some branch systems bore clusters of large, terminal sporangia in their apical parts (Fig. 1). There is also a repetition of the form of the primary xylem column in successive parts of the branch system (Figs. 3, 4, 13). The primary xylem strand in *Tetraxylopteris* differs from that of *Aneurophyton*, however, in being 4-lobed instead of 3-lobed, and the vascular strands to lesser divisions of the branch systems depart in an opposite and decussate fashion rather than in a spiral manner (Fig. 13).

The secondary wood is similar to that of *Ancurophyton*. Tracheids are pitted with crowded, circular-bordered pits on radial (Fig. 5) and tangential walls. Rays seem to be both uniseriate and multiseriate and range from low to very high. Perhaps the more interesting secondary tissue is the phloem. It is characterized by at least 3 types of cells—thick-walled fibers in clusters or radial rows, thin-walled, empty-looking, elongate parenchyma cells, and clusters of very elongate cells with very thick walls of irregular thickness (Fig. 6). I have previously suggested that these latter cells might be the sieve cells (Beck, 1957). This is certainly a remarkable tissue, and in complexity of organization it is comparable with that of living gymnosperms.

We do not know that *Tetraxylopteris*, like *Ancurophyton*, was a large tree, but it was certainly a good-sized woody plant, and quite possibly of arborescent stature.

Archaeopteris-Callixylon—The dominant arborescent type of the Upper Devonian was very probably *Archaeopteris*. This plant is represented by two organ genera, *Archaeopteris*, the foliage, and *Callixylon*, the stems, roots, and isolated secondary wood. Both of these genera have been known for many years as characteristic of Upper Devonian strata in Europe and North America, often occurring together in the same localities. It was not until 1960, however, that these organs were discovered to be parts of the same plant (Beck, 1960a, 1960b).

I conceive of this plant as being similar in habit to that of modern coniferophytes with a straight, main axis from which branch numerous smaller branches (Fig. 11) (See Beck, 1962). Unlike either *Ancurophyton* or *Tetraxylopteris*, however, it bore bipinnately compound, laminate leaves, some of which produced numerous, rather large sporangia in their basal parts (Fig. 12). At least one species, *A. latifolia*, described by Arnold (1939), is known to have been heterosporous.

In internal structure this plant is rather remarkable. In the stem a large pith is bounded by a cylinder of collateral primary vascular strands outside of and in contact with which the secondary xylem was formed. Primary xylem is mesarch. The single leaf traces depart as simple branches from what seem to be discrete vascular stands, and, consequently, there are no leaf gaps (Fig. 10) (See also Arnold, 1930).

Secondary xylem consists only of tracheids and rays (Figs. 7-9). The tracheids are pitted on their radial walls only, except in areas of late wood. Circular bordered pits occur in horizontally aligned groups, in one to several vertical rows, and one species (Beck, 1962b) is characterized by uniseriate pitting (Figs. 7, 9). The rays vary from very low to very tall and

from uniseriate to biseriate, rarely multiseriate. Characteristically, however, rays in the genus are relatively low and narrow. The most striking feature of the rays is the presence of ray tracheids which are very conspicuous in some species (Figs. 7, 8).

It is obvious that these three plants share characteristics often associated with several groups. *Aneurophyton and Archaeopteris* have been classified with the Filicineae by some workers. All have been also either classified with some group of gymnosperms or considered to be ancestral to some gymnosperms. These plants have been called fern-like trees for the benefit of this symposium, but they could equally well, or perhaps more appropriately, be called gymnosperm-like trees.

I should like now to emphasize their features which are commonly characteristic of certain major groups, considering together first the characteristics of *Aneurophyton* and *Tetraxylopteris*.

1. *Psilophyte-like characters:* possession of leaf-like branch systems and the absence of true leaves, pteridophytic reprodnction, large terminal sporangia, and possession of a protostele.

2. *Fern-like characters:* branch systems instead of true leaves (some coenopterids), pteridophytic reproduction, large terminal sporangia (some primitive genera), mesarch primary xylem, and the possession of a protostele (coenopterids and some primitive filicinean genera).

3. *Gymnosperm-like characters:* mesarch primary xylem (some primitive pteridosperms and cordaites), secondary growth and arborescent habit, circular bordered pits, complex secondary phloem with fibers in *Tetraxylopteris*.

It is instructive to note that most characteristics of these genera that can be considered fern-like are also psilophyte-like. Mesarch primary xylem, considered to be characteristic of ferns also occurs in some primitive pteridosperms and cordaites. And it should also be noted that some primitive gymnosperm seed-like fructifications, such as *Genomosperma*, recently described by Long (1959), are really intermediate between the pteridophytic condition and the true seed habit. The protostele is characteristic of certain primitive gymnosperms such as *Tristichia* (Long, 1961), *Tetrastichia* and *Heterangium*.

It is apparent, therefore, that these characteristics are not especially distinctive of any particular group of plants, but are generalized features, most of which characterize the Psilopsida as well as the primitive members of several other major groups including the Sphenopsida, Filicineae and Gymnospermae.

In regard to the gymnosperm-like characters, mesarch primary xylem

occurs in some primitive gymnosperms, but is certainly more characteristic of ferns. Secondary growth and the arborescent habit are, however, more characteristic of gymnosperms. Although they, as well, characterize some members of all major groups, they are of rare occurrence among the ferns, and of general occurrence among gymnosperms. Circular bordered pits are of very rare occurrence in ferns, and of the 3 or 4 extant genera of ferns which produce secondary xylem, only the genus, *Botrychium*, is characterized by secondary tracheids with circular bordered pits.

The complex phloem of *Tetraxylopteris*, containing fibers, seems to be most similar to that of the gymnosperms. No other group of Paleozoic plants, or for that matter recent plants except angiosperms, produced such complex secondary phloem.

Let us now consider the characteristics of *Archaeopteris*. It is clear that this plant is much more highly advanced than either *Aneurophyton* or *Tetraxylopteris*. But it has, like them, certain generalized primitive features such as mesarch primary xylem and pteridophytic reproduction. It bore large leaves, some of which, in their basal parts, produced groups of large sporangia on non-laminate fertile pinnules. This condition is similar to that of some coenopterid ferns, and to the pollen-bearing fructifications of some pteridosperms.

The most striking features of the genus and those which perhaps most accurately suggest its true taxonomic affinities are found in its internal structure which is extraordinarily gymnosperm-like.

The primary vascular system, a eustele of collateral bundles; the origin of the trace as a single strand; and the absence of a leaf gap[2] are all highly characteristic of the gymnosperms. And, significantly, there is no other group with this combination of characters.

The secondary wood is so similar to that of the coniferophytes that it has often been suggested that *Callixylon* might have been a seed-producing member of this group. The large circular-bordered pits in a uniseriate arrangement in one species is very similar to that of some cordaites and many conifers, as is the restriction of tangential pits to late wood tracheids, and the numerous, small rays of most species. Ray tracheids are found elsewhere only in the conifers.

Now that we have considered the important morphological and anatomical characteristics of these woody, fern-like plants, we are ready to attempt to answer the questions raised at the beginning of this paper.

[2] Strong evidence presented by Kumari (1963) suggests that there have never been leaf gaps in the conifers, some other gymnosperms and their probable precursors, and that stelar evolution in ferns and gymnosperms comprises two entirely separate lines.

1. *Do these plants represent a primitive fern stock, or direct ancestors of the ferns?* If so, they must possess characters of the ferns, or characters from which those of ferns could logically have evolved. We have seen that *Aneurophyton*, *Tetraxylopteris* and *Archaeopteris* do have some of the generalized characteristics of primitive plants, but that these are not features which are necessarily distinctive of ferns.

Characters such as circular-bordered pits in all three genera, and the eustele of collateral primary vascular bundles in which there are no leaf gaps in *Archaeopteris*, are not generally characteristic of the ferns which, instead, most often possess scalariform pits and, when siphonostelic, dictyosteles of concentric primary vascular strands. There are, of course, leaf gaps, and one or two traces may originate separately from the vascular cylinder whereas in most gymnosperms the leaf trace originates as a single strand. We know, too, from the studies of Bailey, Frost, and others that in the Pteropsida the trend in pit evolution seems to be from the scalariform to the circular-bordered, and no positive evidence of a reverse trend from circular to scalariform-bordered has been presented. Consequently it is reasonable to conclude that these three woody, fern-like genera of the Upper Devonian were neither primitive ferns nor fern ancestors.

2. *With what groups do they show the closest phylogenetic relationship?* When one considers the morphology of *Aneurophyton* and *Tetraxylopteris*, with their non-laminate branch systems, large terminal sporangia, protostelic vascular column, the repetition of structure in successive branch orders, and the dense, uniform pitting on tangential as well as radial walls of the secondary tracheids, he cannot avoid the conclusion that these are relatively primitive plants. They exhibit, in so many ways, a psilophytic organization that if it were not for their more complex branching patterns and their secondary tissues of a gymnospermous type they could be properly classified as psilophytes. Therefore, it seems logical to suggest that these plants might have evolved directly from some psilophytic type rather than from any group of primitive ferns. It is possible, of course, that this psilophytic group was also ancestral to the Devonian ferns. The circular-bordered pits of *Aneurophyton* and *Tetraxylopteris* and the complex secondary phloem of the latter suggest that these plants were in the gymnospermous line of evolution.

Archaeopteris is, I believe, rather closely related to the primitive gymnosperms. It and other similar Upper Devonian and Lower Mississippian plants might have originated from groups similar to *Aneurophyton* and *Tetraxylopteris*, but it has evolved to a level very close to that of the lyginopterids and cordaites. In some ways it was probably more advanced

than they. Those features which do not conform to the morphology of the ferns such as the eustele of collateral bundles, leaf traces originating as single strands, absence of a leaf gap, the common occurrence of small uniseriate rays, some containing ray tracheids, circular-bordered pits sometimes arranged in a uniseriate manner, are all characteristic, some of them distinctive, of gymnosperms, and most especially, of the coniferophytes.

3. The third question, "Have they given rise to any major groups of plants?", hardly needs further answer. I must emphasize that no one knows just what groups, if any, have been derived from the particular genera discussed in this paper, but I believe we can conclude with confidence that these plants are neither ferns nor fern ancestors, but rather represent a large group of progymnosperms which might include other, lesser known genera such as *Calamopitys*, *Stenomyelon*, *Diichnia*, an undescribed New Albany shale genus, *Sphenoxylon*, *Protopitys*, *Cauloxylon*, *Endoxylon*, *Eristophyton*, *Pitys*, and others from which the gymnosperms have evolved. I predict that when we learn more about this group of progymnosperms, it will be found to contain two or more distinct groups, all arising from the Aneurophytales, and each representing an evolutionary line leading to a major group of gymnosperms.

In my opinion, the woody, fern-like trees of the Devonian, *Aneurophyton*, *Tetraxylopteris* and *Archaeopteris*, probably do not have a close phylogenetic relationship with the ferns, and have not been significant in fern origin and evolution.

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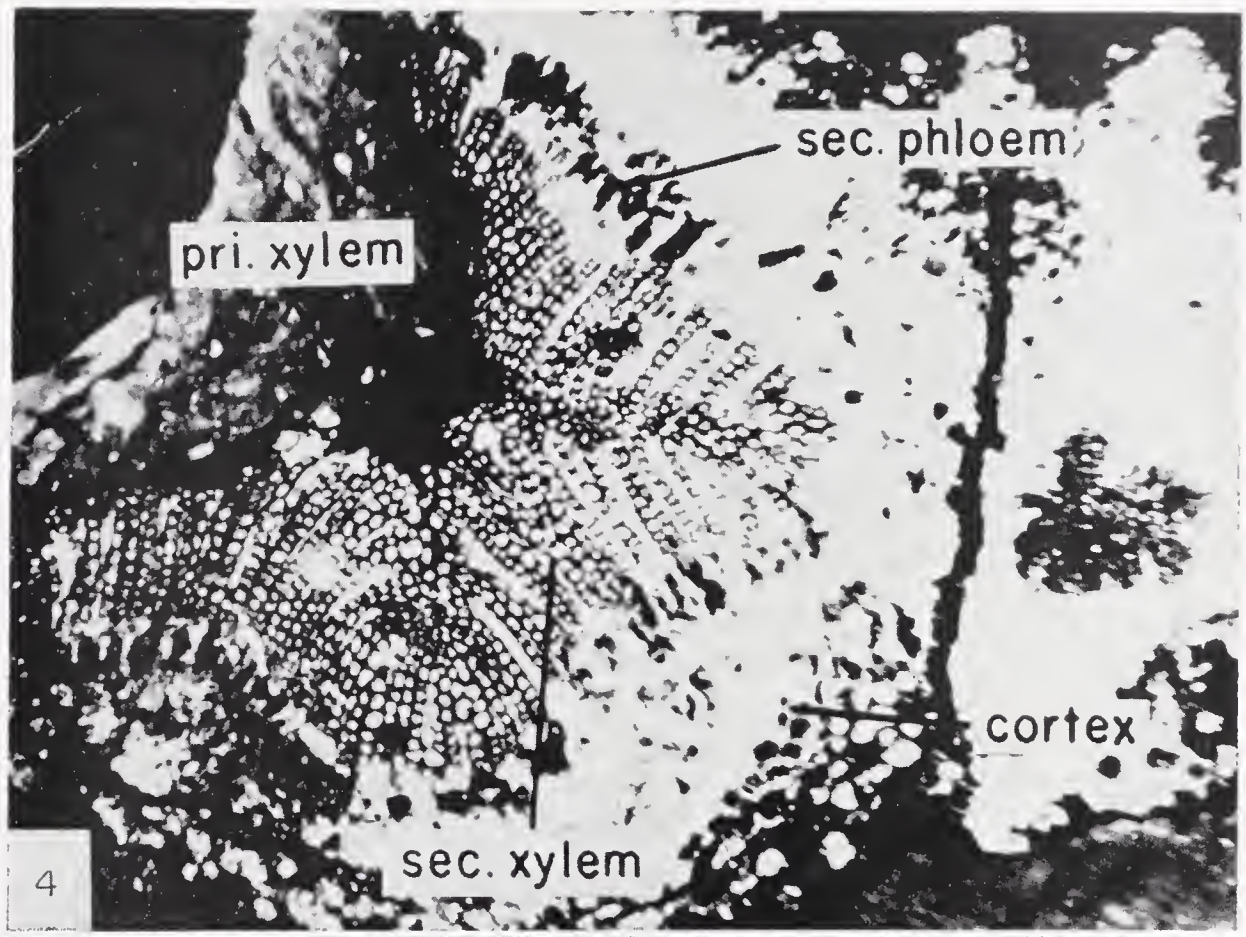
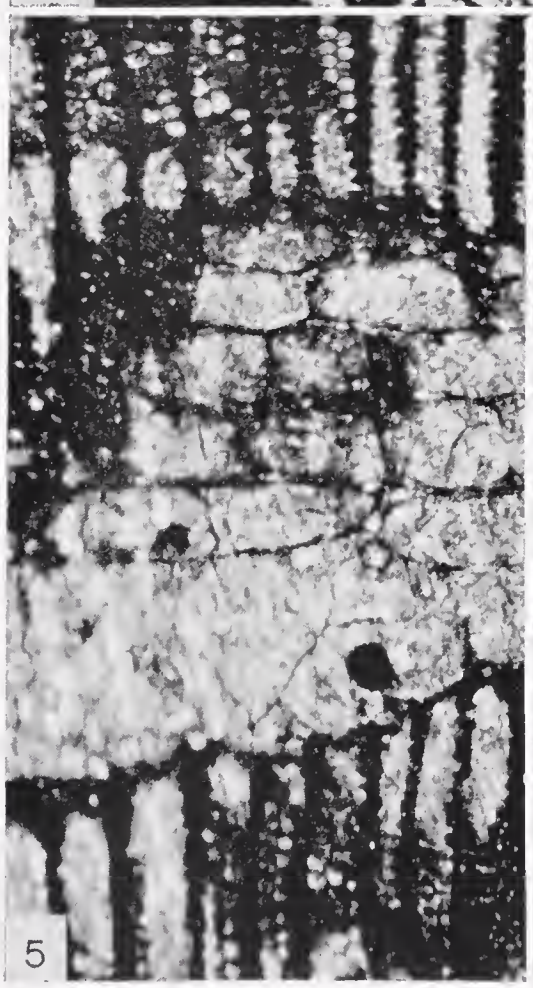
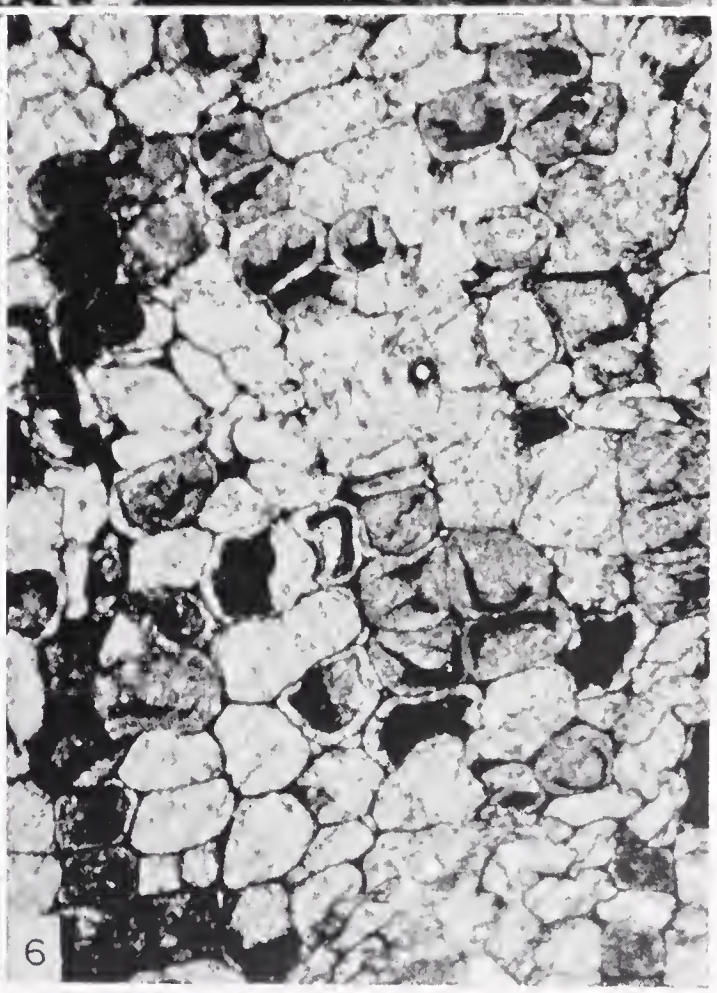
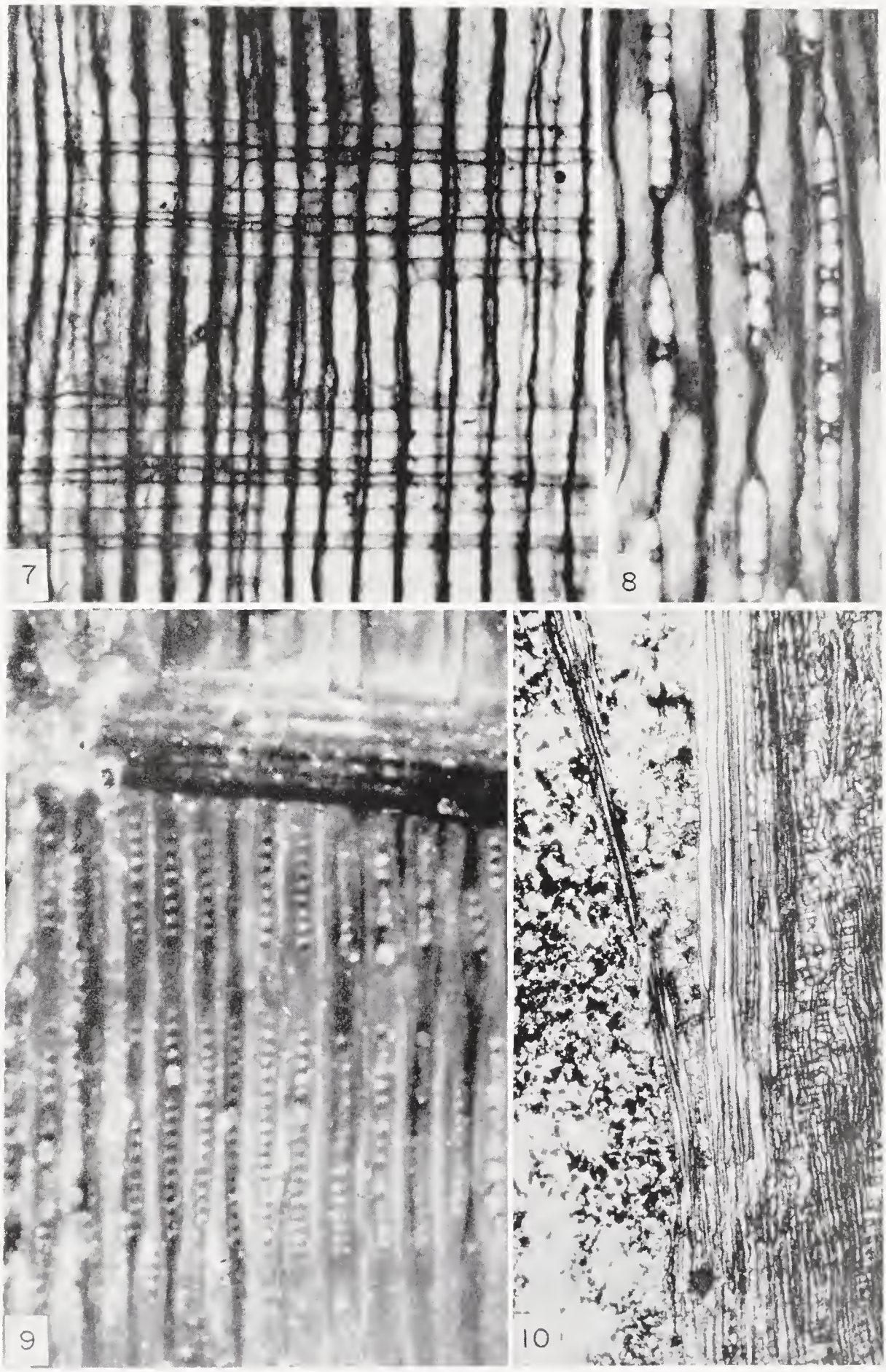
FIGS. 1-3: Fig. 1. *Tetraxylopteris*. Parts of vegetative and reproductive (lower left) branch systems. X 1. Fig. 2. *Callixylon*. Partially reconstructed stump, on campus of East Oklahoma State College, Ada, Oklahoma. Fig. 3. *Tetraxylopteris*. Transverse section of an axis in a branch system showing the formation of a xylem strand cruciform in section. X 50.



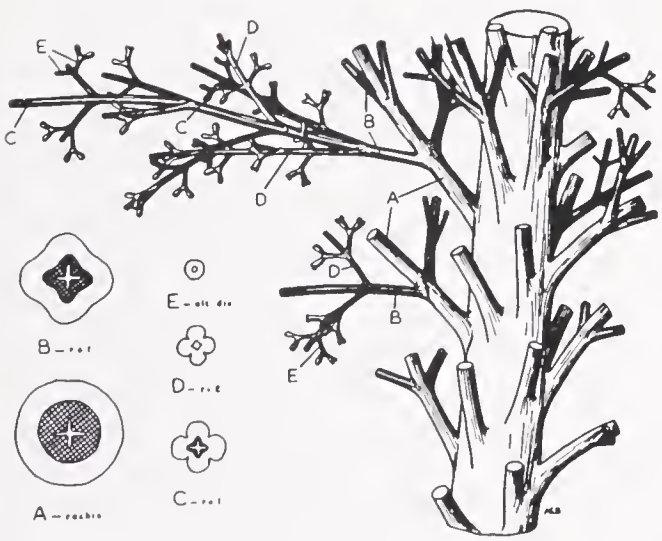




FIGS. 4-6: *Tetraxylopteris*. Fig. 4. Transverse section illustrating the form and pattern of primary and secondary tissues in axes of a branch system. The primary xylem strand in the smaller axis (at right) is similar in form to that in fig. 3, and is surrounded by a small amount of secondary xylem. X 40. Fig. 5. Radial section showing ray and crowded circular-bordered pits. X 140. Fig. 6. Transverse section of heterogeneous secondary phloem. X 140.



FIGS. 7-10: *Callixylon*. Fig. 7. Radial section of *C. crianum* showing multiseriate circular-bordered pits and ray tracheids. X 100. Fig. 8. Tangential section of *C. crianum*. X 100. Fig. 9. Radial view of *C. arnoldii* showing uniseriate pits in horizontally aligned groups. X 100. Fig. 10. Longitudinal section through vascular bundle of *C. crianum* showing origin of leaf trace (on right, in contact with secondary wood) and continuing reparatory strand (on left). X about 25. (Negative supplied by Professor C. A. Arnold).



FIGS. 11-14: Fig. 11. *Archaeopteris*. Habit reconstruction. Fig. 12. *Archaeopteris*. Reconstruction showing segment of a branch and parts of 3 leaves. (Figs. 11 and 12 from Beck, 1962a.) Fig. 13. *Tetraxylopteris*. Reconstruction of part of an axis bearing the basal parts of radially symmetrical branch systems. Diagrams of transverse sections show the repetition of form of the primary xylem strand in several orders of branching. (Slightly modified from Beck, 1957.) Fig. 14. Reconstruction of *Eospermatopteris* as originally interpreted by Goldring. (Photographically modified from Goldring, 1924.)

The question of the phylogenetic position of the Coenopteridales[1]

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Introduction. The order Coenopteridales is made up of ferns that are not referable to any living group and are found in strata ranging in age from Devonian to Permian. Coenopterids are generally monostelic in contrast to those extinct plants placed in the order Cladoxylales which are usually polystelic. Coenopterids are usually relatively small and almost all of them lacked secondary xylem. These two features distinguish them from the majority of the fossil fern order Protopteridiales which were arborescent and had abundant secondary xylem. Aside from these few generalizations, it is impossible to state very exactly just what a coenopterid fern is like. This is essentially because of the artificiality of the order, which is now almost universally recognized as showing as much morphological diversity as exists among the major groups of living ferns. Therefore, we are not discussing the phylogenetic position of one group of plants, but rather of several groups in this paper. It should be emphasized, however, that due to the very poor understanding we now have of the major lines of evolution of ferns it is most convenient to retain the order.

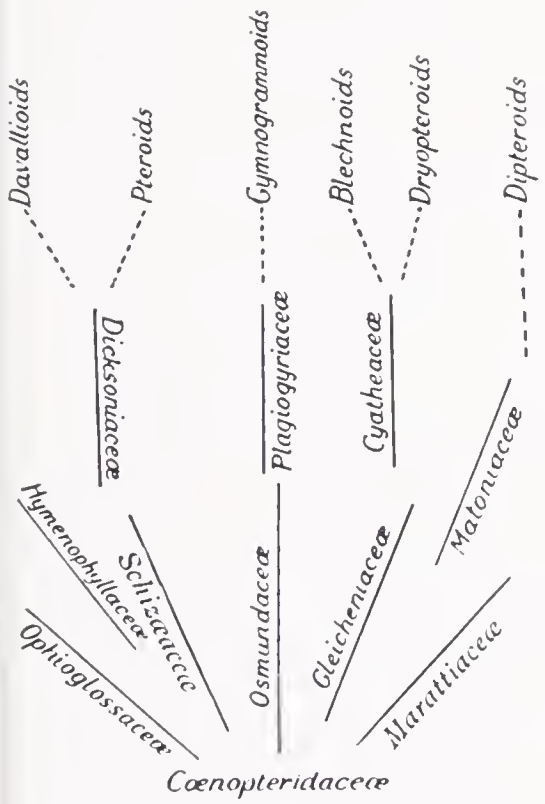
Most of the fossil remains of coenopterids are vegetative parts, although some fertile parts are known, and these are very fragmentary. The most commonly found parts represent the portion of the plant which is equivalent to the frond of living ferns. Generally, the plants in the order are incompletely known, and in only a few species has the structure of the whole plant been determined. This very incomplete knowledge of most of the forms has led to various artificial systems of classification, usually based on relatively few anatomical features, such as the symmetry and structure of the leaf trace, and the symmetry of the frond. This emphasis upon anatomical features in determining relationships in the order is in marked contrast to the situation in living ferns where the structure, arrangement, and position of the sporangia have provided the most reliable indications of natural relationships.

Numerous systems of classification have been suggested for the coenop-

[1] I wish to thank Professor T. Delevoryas for providing me with facilities in the Department of Biology, Yale University, during the period in which this manuscript was completed.

terids. A recent system (Morgan and Delevoryas, 1954) which seems to be somewhat more natural than most of the previously suggested ones, will be used here and delimits four families: Stauropteridaceae, Zygopteridaceae, Botryopteridaceae, and Anachoropteridaceae. I should point out that in some cases these familial groups are more convenient than they are natural; however, for our present purposes emphasis will be placed on the features of the families.

The coenopterids have caught the interest of many workers because they appear to have a position intermediate between psilophytes and certain Devonian fern-like plants, and living ferns. Various ideas concerning the phylogenetic position of the Coenopteridales have been proposed. Those of Bower (1935) represent an older and widespread point of view which is still generally presented in textbooks of botany and plant morphology. In Bower's opinion, the Coenopteridales (which are all referred to a single family by him) (Fig. 1) represent the ancestral group from which all of the major lines of present day ferns have evolved. Even when Bower proposed



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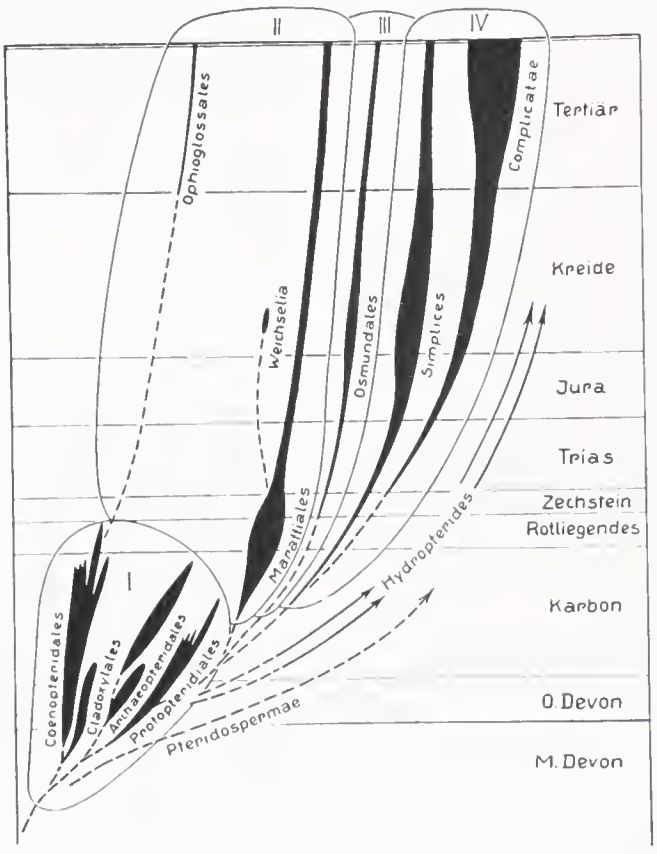

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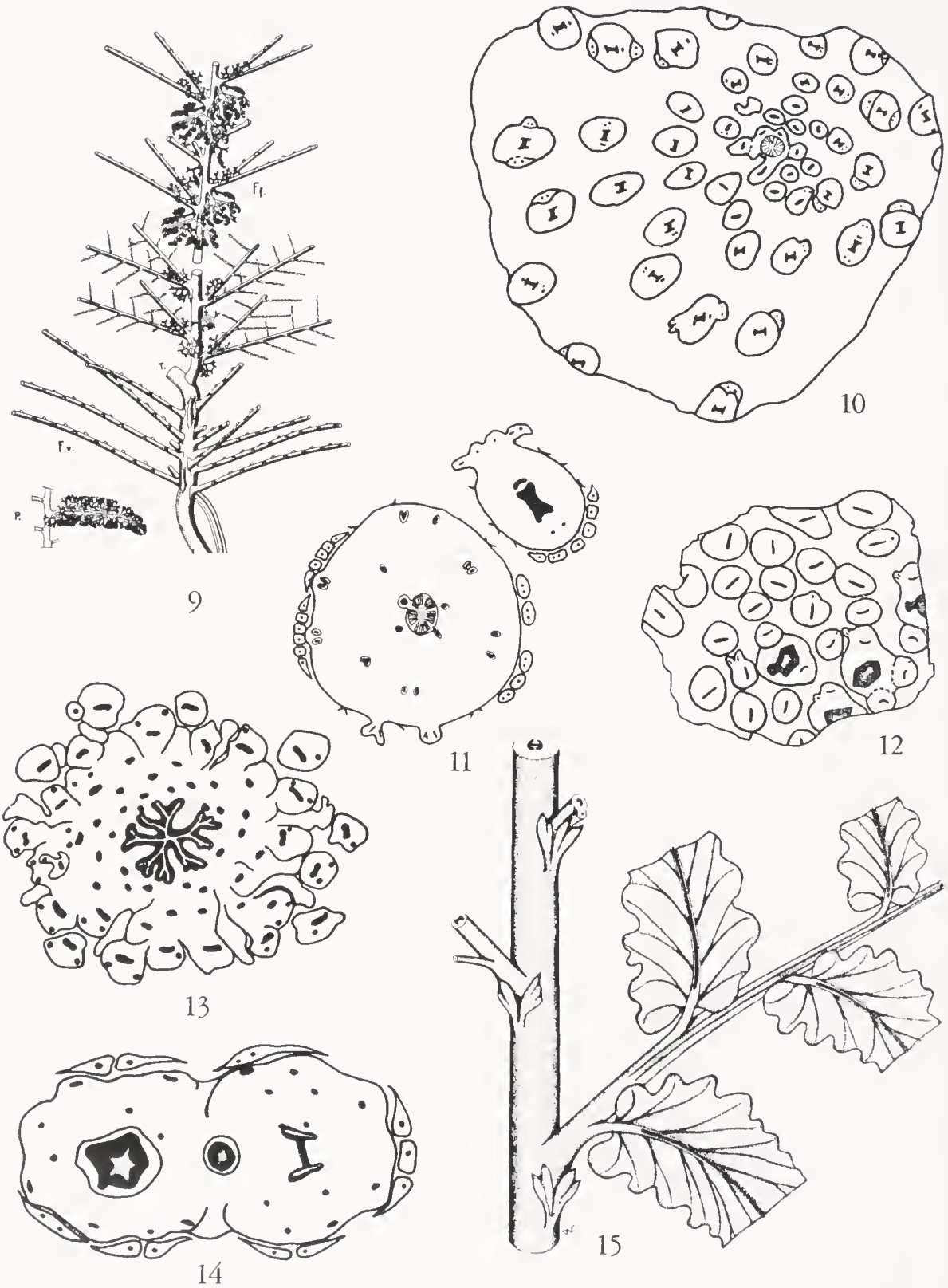
FIGS. 1-2. Two representative views concerning the phylogenetic position of the coenopterid ferns. Fig. 1. According to Bower (From Bower, 1935, by permission of Macmillan & Co.). Fig. 2. According to Zimmermann (From Zimmermann, 1959).

FIGS. 3-8. *Stauropteris oldhamia.* Fig. 3. Idealized reconstruction of a portion of the aerial system (From Delevoryas, 1962). Fig. 4-8. Cross sectional configurations of the xylem at several successively higher levels in a branching system. Protoxylem indicated in white, the small terete vascular strands in the figures belong to aphlebiae

these ideas, however, evidence was available that several families of modern ferns were at least in part contemporaneous with the coenopterids, and the early fossil records of these families has become much more firmly established in the intervening years. The families Schizaeaceae, Gleicheniaceae, and the extinct family Psaroniaceae of the order Marattiales are now known from the Carboniferous, while the family Osmundaceae is known from the Permian period. Nothing is known of the vegetative anatomy of the earliest members of the Gleicheniaceae and Schizaeaceae, and some early osmundaceous forms resemble certain plants included in the Coenopteridales, as will be mentioned in more detail later. Whereas the earliest members of the Schizaeaceae and Gleicheniaceae are known only from leaf material bearing the characteristic sporangia of the families, the psaroniaceous tree ferns are known from spore producing parts resembling those of the Marattiaceae, and from vegetative remains as well. These early marattialeans show little similarity to the generally small coenopterids which had relatively simple internal anatomy. They are large plants with highly dissected vascular systems which are often polycyclic dictyosteles; these features suggest a long evolutionary history prior to the Carboniferous period about which we know nothing at present.

Information concerning these ferns which were members of living groups, and the failure to find ancestral forms from among the coenopterids for any living group, have led to phylogenetic schemes in which the coenopterids are not considered ancestral to the majority of ferns. One such system is that of Zimmermann (1959) (Fig. 2). This viewpoint is very different from that of Bower, and represents a major change in the interpretation of the structures found in the order. To understand the reasons for this change in view we will now consider in some detail each of the four families included in the order. In this discussion we will concentrate upon the overall level of organization of the vegetative and reproductive parts of each of the families by using several representative members of each as examples. Because the information concerning the fertile parts is much less complete, it will be presented for all of the families after the discussion of the vegetative structure. It should be emphasized that the information presented here has been obtained over many years and by numerous workers, and that little is original with the present writer, who

subtending the various orders of laterals. Fig. 4. A typical configuration in a large axis near the base of the branching system. Fig. 5. A level where a pair of primary lateral axes are borne by a large axis. Fig. 6. A level in a primary lateral where a pair of secondary laterals are borne. Fig. 7. A level in a secondary lateral where a pair of tertiary laterals arise. Fig. 8. A tertiary lateral where a pair of ultimate branches arise. (Redrawn with modifications from Bower, 1926).



FIGS. 9-15. The family Zygopteridaceae. Fig. 9. Reconstruction of *Rhacophyton zygopteroides*. The stem (T) bears fronds of two types which are indicated by F.f. (fertile frond), and F.v. (vegetative). P indicates a reconstructed pinna of a sterile frond. (From Leclercq, 1951). Fig. 10. *Zygopteris primaria*. Cross section of the stem and surrounding zone of leaf bases. (Redrawn from Sahni, 1932a). Fig. 11.

is attempting to review the most important features of coenopterids that should be of interest to people concerned with ferns and their evolution.

The structure of vegetative parts. STAUROPTERIDACEAE. *Stauropteris*, the single genus in this family, is known from two species: *S. burntislandica*, which is of Lower Carboniferous (Mississippian) age, and *S. oldhamia*, which is from the Upper Carboniferous (Pennsylvanian). The genus appears to have been composed of relatively small plants with a bushy appearance (Fig. 3). Anatomically, axes are essentially stem-like, with a slight bilateral symmetry present in the vascular system (Fig. 4) that consists, in the larger axes, of four separate groups of mesarch primary xylem alternating with areas of phloem. Axes bear alternating pairs of branches that resemble the parent axes internally. Repetitive branching occurs for a variable number of times with the daughter axes always being smaller than the parent (Fig. 3). The vascular system is also smaller in the distal parts of the system and is simpler in configuration (Figs. 5-8), and the ultimate branchlets are very narrow and contain terete protosteles (Fig. 8). All axes that have been found thus far are stem-like and are apparently part of a determinate three dimensional branching system. This system may be interpreted as representing a stage in the evolution of the frond, or megaphyll. On the other hand, the failure to discover a distinct stem, even after very many specimens of the genus have been found, may indicate that the plant lacked a differentiation into definite stem and frond areas. If this proves to be the case, *Stauropteris* would be most unlike any living fern and unlike the rest of the Coenopteridales.

The primary xylem is composed of scalariform tracheids and resembles that of many modern ferns.

ZYGOPTERIDACEAE. This family is the largest in the order and has the longest geological history (Devonian to Permian). Forms such as *Rhacophyton zygopteroides* (Fig. 9), *Zygopteris illinoiensis* (Fig. 11), and *Ankyropteris glabra* (Fig. 14) had slender, elongate stems, often with distantly spaced leaves, and may have been procumbent or scrambling plants. Other forms with leaves closely arranged about a stout stem, such as *Zygopteris primaria* (Fig. 10), and *Asterochlaena laxa* (Fig. 13), probably had an upright habit resembling that of modern species of the genus *Osmunda*, and were relatively large plants. *Clepsydropsis australis* (Fig. 12) has an

Zygopteris illinoiensis. Cross section of the stem and lower portion of a petiole. Fig. 12. *Clepsydropsis australis*. Cross section of a small portion of a false stem. (Redrawn from Sahni, 1928). Fig. 13. *Asterochlaena laxa*. Cross section of the plant. (Redrawn with modifications from Bertrand, 1911). Fig. 14. *Ankyropteris glabra*. Cross section of the stem, base of petiole, and axillary branch stele. Fig. 15. *Ankyropteris glabra*. Reconstruction of a portion of the frond. (From Eggert, 1963).

interesting "false stem" made up of numerous relatively small and dichotomously branching stems bearing petioles. These individual stems and leaf bases form a large and compact structure which superficially resembles a single large stem. The entire structure which we term a "false stem" closely resembles similar conditions which occur in other ferns such as the Cretaceous genus *Tempskya*, and the living genera *Hemitelia* (Cyatheaceae), and *Todea* (Osmundaceae).

Members of the Zygopteridaceae fall into two groups on the basis of the structure of their fronds. In the so-called Etapterideae primary pinnae occur in alternating pairs along opposite sides of the petiole. This type of frond with four ranks of primary pinnae is said to be quadriseriate. In the Clepsydrideae the petioles bear two ranks of primary pinnae as in living ferns. It should be pointed out that, although we use the term frond to refer to that part of the zygopterid plant body that appears to be equivalent to the frond of living ferns, in most cases this zygopterid frond is not anatomically similar to the leaf of a living fern. Usually it is three dimensional with the various orders of pinnae lying in several planes rather than in one plane as in living ferns. Also, the fronds of many zygopterids may have lacked planated foliar areas. A lack of information about the distal parts of most zygopterid leaves forces us to use caution in generalizing about this possible feature of zygopterid fronds.

Zygopterid stems usually have actinosteles which are either mesarch or exarch and which may be roughly star-shaped, as in *Ankyropteris* (Fig. 14) and *Clepsydropsis* (Fig. 12), or very deeply lobed, as in *Asterochlaena* (Fig. 13) and *Asteropteris*. In general, a central area of parenchyma and tracheids is present in the stele. The genus *Zygopteris* is unusual in having secondary xylem present about the central primary zone of tracheids and parenchyma (Figs. 10, 11). Secondary xylem is very rare in ferns and occurs in living genera only in *Botrychium* of the Ophioglossales. For this reason, and the similarity of vascular pitting in the genus *Zygopteris* and some members of the Ophioglossales, close natural relationships between the Zygopteridaceae and the Ophioglossales have been suggested. In other anatomical features, however, the two groups are very distinct and these two points of similarity are most likely an instance of convergence.

Rhacophyton zygopteroides (Leclercq, 1951) is the best known Devonian member of the family. As reconstructed, an elongate stem bears fronds of two types (Fig. 9): a fertile frond, and a sterile one. The sterile frond consists of a petiole bearing two ranks of primary pinnae as in modern ferns. However, the remaining portion of this frond is unlike anything found in extant ferns. Each primary pinna axis bears small,

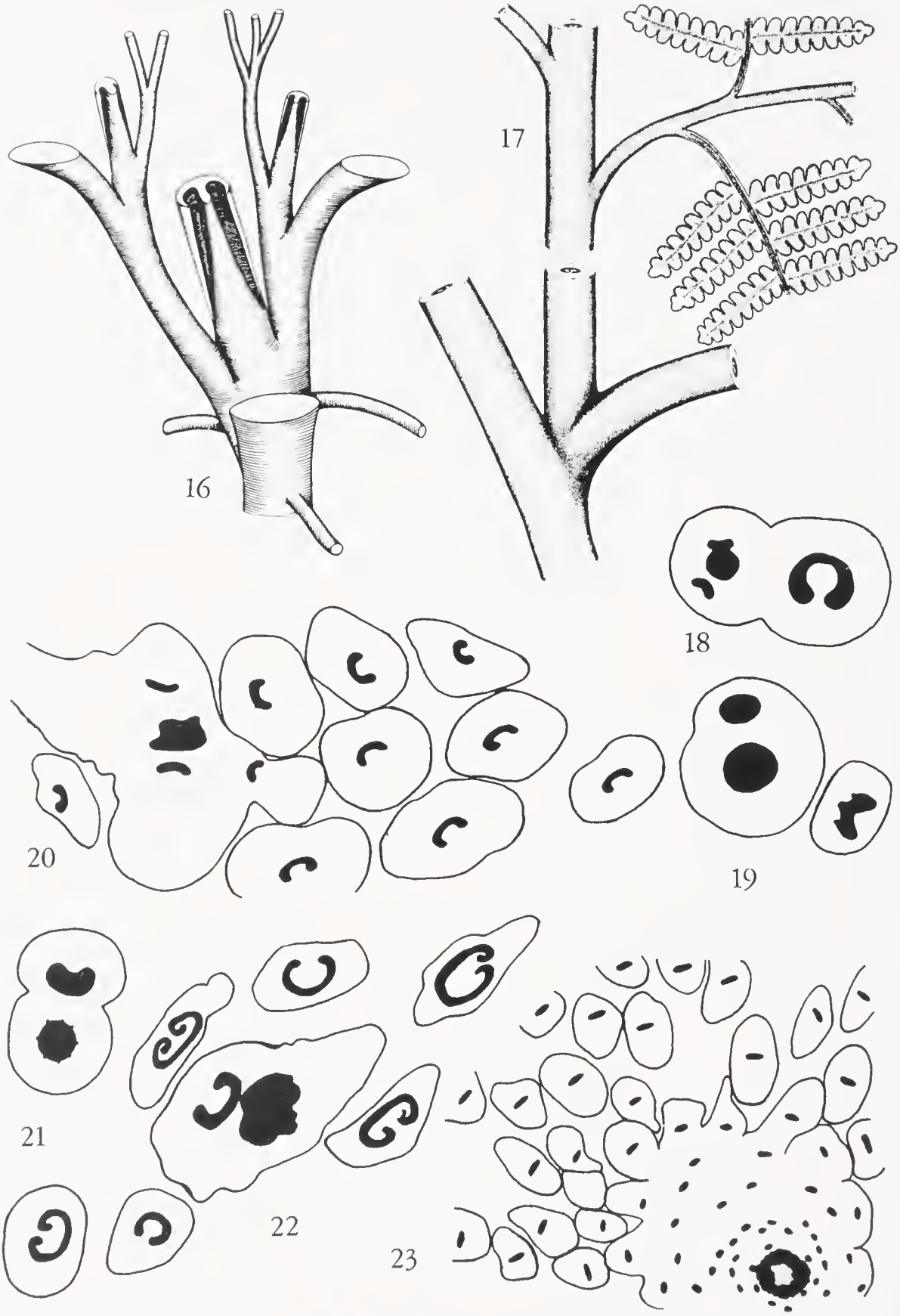
dichotomously ramifying systems of branch-like nature in a helical arrangement, so that the entire pinna system (Fig. 9, P) must have had a very bushy appearance. This is similar to some branching systems in the Cladoxylales.

The fertile frond is larger and more complex than the sterile and has four ranks of primary pinnae arising in pairs from opposite sides of the petiole (Fig. 9, F.f.). Each of these primary pinnae bears secondary pinnae in two ranks, and these have appendages like those of the primary pinnae of the sterile frond. At the base of each primary pinna is a small, fertile area made up of a series of stem-like branched axes, and elongate sporangia are borne at the tips of the ultimate branchlets. This sporangial position is typical of many psilophytalean plants, but is unlike anything in living ferns.

Rhacophyton, then, is an Upper Devonian plant that is quite distinct from the Psilophytales, has definite fern-like vascular anatomy, and shows the early origin of the zygopteridean type of plant. Like the psilophytes it lacks foliar laminae, and its sporangia are terminal on stem-like axes. The fronds show their origin from branching systems very clearly, but there is a distinct differentiation of the plant body into stems and leaves.

It is often stated that the zygopterid leaf is primitive and intermediate between a branching system and a true megaphyll. This, however, is an overgeneralization. The vascular systems of petioles often possess adaxially and abaxially directed arms or antennae (see Figs. 10, 11, 14, 15) which may be variously shaped and curved, and the structure of this system is often very elaborate. It appears that progressive elaboration of the vascular system is a feature of zygopterid leaf evolution, and anatomically the leaves of many forms appear to be more highly specialized than the typical leaf of modern ferns. We cannot, therefore, refer to the zygopterid leaf as an entirely primitive structure and it is now known that at least one species, *Ankyropteris glabra*, had a leaf essentially like that of a modern fern (Fig. 15). The petiole of this plant bears two ranks of primary pinnae and has typical zygopterid internal anatomy, while the primary pinnae bear secondary pinnae with broad foliar regions. The entire leaf was two dimensional and the various orders of pinnae were oriented in essentially the same plane.

Axillary branching in *Ankyropteris glabra* is another interesting feature of this plant, and one that is very rare in ferns, both living and fossil. The axillary branch (Fig. 14) develops into a typical stem and bears leaves above the level of its separation from the parent stem (Eggert, 1959a). It is doubtful whether this occurrence of axillary branching in a



FIGS. 16-23. Fig. 16. *Botryopteris triseeta*. Xylem system of a part of the stem

zygopterid fern indicates any close relationship between the zygopterids and those living ferns having axillary branching such as *Trichomanes* (Hymenophyllaceae) or *Botrychium* (Ophioglossaceae).

Tracheids of members of the family generally have multiseriate scalariform, or circular bordered pitting; exceptions are the genera *Rhacophyton*, *Ankyropteris*, *Clepsydropsis*, and *Asterochlaenopsis*, in which scalariform tracheids resembling those of most living ferns are present (this excludes the Osmundaceae, in which pitting is predominantly multiseriate scalariform, and the Ophioglossaceae, which have circular bordered pitting).

Botryopteridaceae. The genus *Botryopteris* is generally placed in a separate family and is distinct in several anatomical respects from other coenopterids. Perhaps the most characteristic feature of the genus is the outline of the traces in foliar axes which generally have three adaxially directed arms of xylem (see, for example, the outlines of the vascular systems indicated on the cut surfaces in Fig. 17). In outline these traces resemble the Greek letter *omega*. In the most completely known species, such as *B. antiqua* (Holden, 1962), or *B. trisecta* (Mamay and Andrews, 1950) upright aerial stems bore lateral branching systems (which we will refer to as fronds) in a helical arrangement. Stems of the genus are usually protostelic, xylem generally lacks parenchyma, and tracheids usually have multiseriate pitting with the individual pits varying from scalariform to circular in outline. Figure 16 illustrates a portion of the xylem system of a stem and frond of *B. trisecta*. A primary axis arising from the stem divides trichotomously; the central member of the three daughter axes develops typical petiolar anatomy at higher levels with the xylem attaining an omegoid outline. The two lateral axes of the trio have the internal structure of stems, trichotomize at a higher level, and, as with the first order of branching, the median member becomes petiolar in structure and the two laterals remain stem-like. Distal tapering of this lateral branching system or frond suggests a determinate manner of growth which is like that of a typical leaf.

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and lateral branching system or frond. (From Mamay and Andrews, 1950). Fig. 17. Reconstruction of the distal part of the frond of *Botryopteris* c.f. *forensis*. (From Delevoryas and Morgan, 1954a). Fig. 18-23. Representative members of the family Anachoropteridaceae. Fig. 18. *Anachoropteris clavata*. Cross section of a petiole bearing a protostelic stem. Fig. 19. *Psalixochlaena cylindrica*. Cross section of the stem illustrating the configuration of the leaf trace in the stem cortex and in the free petiole. (Based on Holden, 1960). Fig. 20. *Tubicaulis stewartii*. Cross section of the stem and surrounding leaf bases. Fig. 21. *Apotropteris minuta*. Cross section of the stem with a leaf trace in the cortex. (Based on Morgan and Delevoryas, 1954). Fig. 22. A specimen having *Anachoropteris involuta* type petioles and a *Tubicaulis* type stem, shown in cross section. (Based on Hall, 1961.) Fig. 23. *Grammatopteris baldaufi*. Cross section of the stem and zone of leaf bases. (Based on Sahni, 1932b.)

It was long thought that *Botryopteris* did not possess any foliar laminae (although a few possible remains of such a nature were described in the older literature). Work by Delevoryas and Morgan (1954a), however, on material probably referable to *B. forensis*, shows very prominent foliar structures. Somewhere on the lateral branching systems, probably in a distal part, the frond had the structure shown in Fig. 17. The lower part of this system exhibits three dimensional branching but all of the axes have petiolar anatomy and show the characteristic omegoid configuration of the xylem. Distally, one of these axes was found to bear a number of laterals alternately, in two ranks. These laterals have omegoid vascular traces and also bear laterals in two ranks, which, in turn, bore pinnules with lobed margins. The distal part of this system is planated, with all of the various orders of lateral axes and the pinnules oriented in one plane. In their distal parts then, the lateral branching systems arising from the stems of *Botryopteris*, which we have referred to as fronds, had all of the basic features of a true megaphyll, while in the more proximal parts of these systems more of the features of a branching cauline system were present. This may be interpreted as representing an intermediate stage in the evolution of a megaphyll from a system of branching stems.

Anachoropteridaceae. Anatomically, the members of this family resemble living ferns more closely than any of the other families in the order. The most unusual structural feature of the family is the abaxial curvature of the leaf traces. This is in contrast to the situation in living ferns where the petiolar vascular systems are curved toward the stem (adaxially) (Figs. 18-22). Members of the family differ markedly in size and form. Such plants as *Apotropteris minuta* (Fig. 21), described by Morgan and Delevoryas (1954), and *Psalixochlaena cylindrica* (Holden, 1960) (previously included in the genus *Botryopteris* as *B. cylindrica*) are small and have relatively distantly spaced leaves. Members of the genus *Tubicaulis* range from large upright forms, such as *T. solenites* (Stenzel, 1889), to somewhat smaller upright species, such as *T. stewartii* (Eggert, 1959b) and *T. multiscalariformis* (Delevoryas and Morgan, 1952), which have relatively stout stems bearing leaves in a 2/5 phyllotaxy, and *T. scandens* (Mamay, 1952), which may have been a scrambling epiphytic form. The genus *Grammatopteris* (Fig. 23), which is generally included in the family, although its leaf traces are mesarcs, was a relatively large plant and had an upright stem with very closely spaced leaves. In cross section numerous leaf traces are seen in the cortex, and the stem is surrounded by an extensive zone of leaf bases.

Members of the family generally have exarch or centrarch protosteles

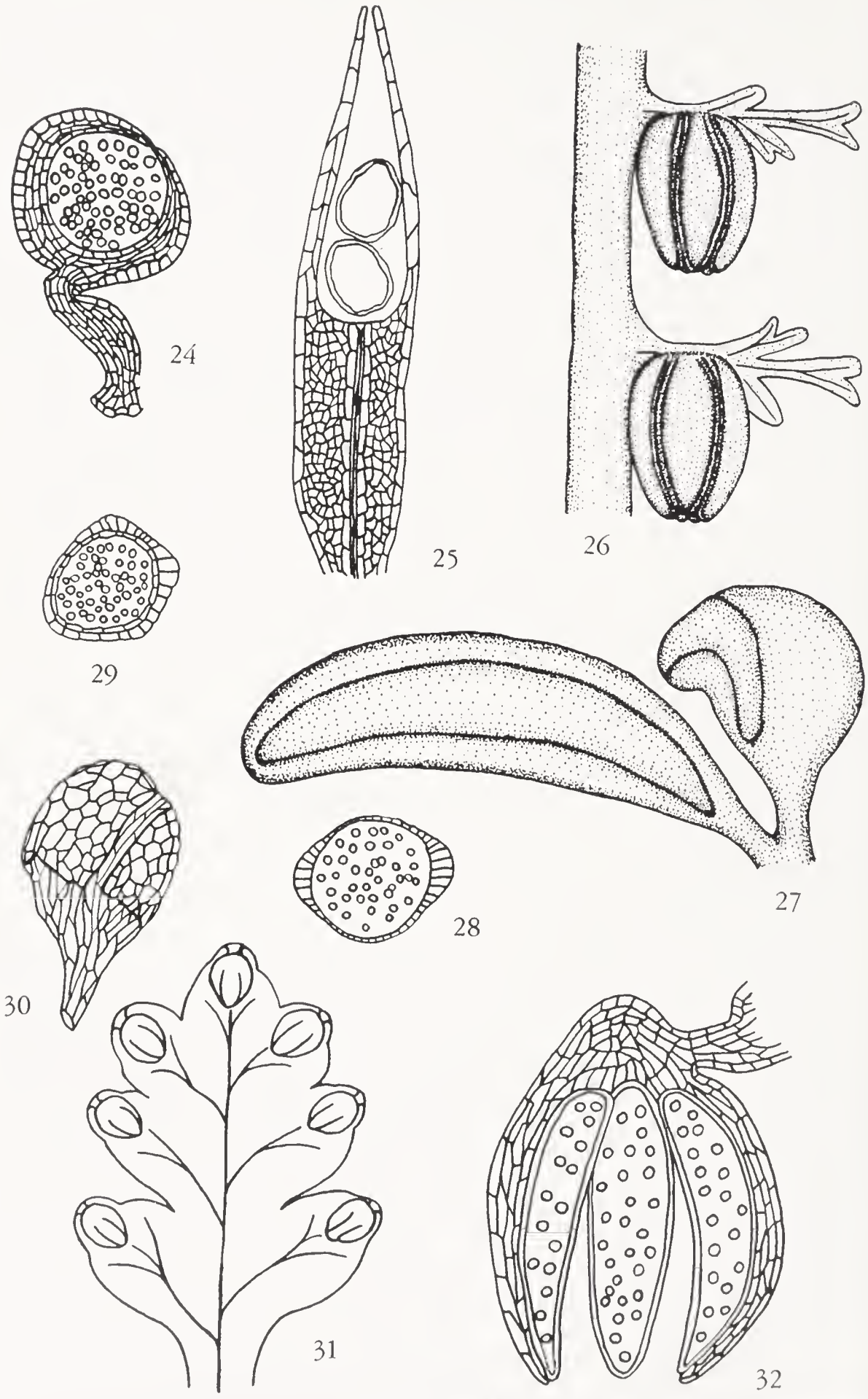
and show varying degrees of curvature in the leaf traces and petiolar vascular systems.

Anachoropteris, the type genus of the family, was known only from frond remains until the recent discovery of stems. The first stems to be found belonged to the species *A. clavata* (Fig. 18) where they were found on certain petioles (Delevoryas and Morgan, 1954b). These petiole-borne stems confirmed the spatial relationships between the leaf traces and the stem stele (a curvature away from the stele) which had been only assumed for a century after the initial description of the genus. More recently, Hall (1961) has described a specimen which apparently represents the mature basal part of a plant having a *Tubicaulis* type of stem which bore petioles of the *Anachoropteris involuta* type (Fig. 21). The specimen suggests that the two genera represent essentially the same type of plant with the generic distinction breaking down in at least one species. The production of plantlets on the leaves of *Anachoropteris* resembles the production of buds and plantlets on the fronds of living ferns such as *Adiantum* (Polypodiaceae), *Anemia* (Schizaeaceae), *Asplenium* (Polypodiaceae), *Scolopendrium* or *Phyllitis* (Polypodiaceae), and *Trichomanes* (Hymenophyllaceae) (Kupper, 1906). One additional coenopterid fern, *Botryopteris hirsuta*, is known to produce buds at the base of a pinna (Long, 1943).

The genus *Grammatopteris* is similar to some early plants referred to the family Osmundaceae. An inner zone of small tracheids in the xylem probably represents a stage in the evolution of a pith, and resembles a similar zone found in the genus *Thamnopteris*, considered to be osmundaceous. In its lower part a leaf trace of *Grammatopteris* also resembles that of some osmundaceous forms but remains incurved, unlike those of members of the Osmundaceae that have pronounced adaxial curvature at higher levels. The general habit of *Grammatopteris* and the multiseriate vascular pitting are also similar to the usual osmundaceous types.

Fronds of members of the family resemble more closely those of modern ferns than those of the other families of the order, and are essentially planated. It should be pointed out, however, that no frond is now known in its entirety, and foliar laminae have not been described for the family. An undescribed specimen apparently referable to *Anachoropteris* has been discovered recently which possesses broad foliar areas on what appear to be secondary pinnae. In the light of this discovery it seems to be very likely that other members of the family will be found to have similar leaf structure.

Structure of spore producing parts. Stauropteridaceae. Plants of the genus *Stauropteris* produced terminal sporangia on the ultimate aerial



FIGS. 24-32. Fertile parts of representative Coenopteridales. Fig. 24. *Stauropteris*

branchlets of the plant. *Stauropteris oldhamia* was probably homosporous and had spherical sporangia with walls several cell layers thick (Fig. 24). Sporangia were exannulate and dehisced by means of an apical pore or stomium. The older species, *S. burntislandica*, was apparently heterosporous (Fig. 25). Megasporangia were first recognized as those of *Stauropteris* by Surange in 1952, although they had been described much earlier, and subsequent study by Chaloner (1958) has shown that each spindle-shaped sporangium usually contains a tetrad of megaspores; two are large and apparently functional, and two are extremely small and were probably abortive. The sporangium lacks an annulus and is merely the swollen tip of a branchlet with the thin-walled sporangial cavity actually occupying less than half of the sporangium. The lower half of the sporangium is solidly parenchymatous and contains a vascular strand. In their position on the plant, and in their histology, the sporangia of both species of *Stauropteris* resemble those of psilophytes more closely than those of living ferns.

Zygopteridaceae. The spore producing parts of almost all zygopterids are unknown, and correlations of several isolated types of fertile parts with genera based on vegetative remains are not definitely proven and must remain only as suggestions at present. In the relatively early form *Rhacophyton zygopteroides* elongate sporangia, the histology of which is not known, were borne terminally on branchlets which were a part of the fertile frond (Fig. 9).

It is likely that certain fertile fronds known from compressions and petrifactions of Pennsylvanian and Permian age belonged to members of the family. These include the genus *Corynepteris*, and material that is variously referred to as *Zygopteris* or *Etapteris lacattei*. In *Corynepteris* (Fig. 26) an individual cluster of closely appressed sporangia (5 to 10) fused only at their bases, occurs on the lower surface of a small foliar area. In the position and arrangement of the sporangia *Corynepteris essinghi* resembles some members of the Marattiales. However, unlike the plants in

oldhamia. Longitudinal section of the sporangium. (Redrawn from Bower, 1926). Fig. 25. *Stauropteris burntislandica*. Longitudinal section of the megasporangium and two megaspores. (Redrawn with modifications from Andrews, 1961). Fig. 26. *Corynepteris essinghi*. Two foliar synangia shown on a small part of the frond. (Redrawn from Zeiller, 1900). Figs. 27-28. *Biscalitheca musata*. Fig. 27. A pair of sporangia. (Redrawn from Mamay, 1957.) Fig. 28. Cross section of a sporangium. (Based on Mamay, 1957.) Figs. 29-30. *Botryopteris globosa*. Fig. 29. Cross section of a sporangium. (Based on Murdy and Andrews, 1957). Fig. 30. An entire sporangium. (Redrawn from Murdy and Andrews, 1957.) Figs. 31-32. *Chorionopteris gleichenioides*. Fig. 31. Reconstruction of a pinnule bearing marginal synangia. (Redrawn from Hirmer, 1927.) Fig. 32. Longitudinal section of a synangium. (Based on several sources.)

that order, a sporangium of *Corynepteris* had a broad vertical annulus on the sides that extended over the tip.

Biscalitheca musata (Mamay, 1957) closely resembles the fertile parts described in the nineteenth century as belonging to the genus *Zygopteris* on the basis of their occurrence on fronds with a quadriseriate arrangement of primary pinnae. Since *Biscalitheca* is more completely known than the *Zygopteris* material described by Renault (1876) it will be considered as a possible additional zygopterid fertile part. The sporangia of *Biscalitheca*

FIG. 33. *Botryopteris globosa*. Section through the entire fructification showing branches of the ramifying system, and terminal clusters of sporangia. X3.3.

(Fig. 27) are banana-shaped and each resembles somewhat the individual sporangium of *Corynepteris*. Two vertical annuli are present on opposite sides of each sporangium which was stalked and located terminally on a small ultimate branchlet of a ramifying system. The whole fructification was relatively large and contained many sporangia. Certain features, such as the wall, which was composed of one cell layer, resemble those of leptosporangiate ferns (Fig. 28), while others, such as the large sporangial size and large spore output, are more like eusporangiate ferns. As presently known, then, some zygopterids appear to have had sporangia on the lower surface of foliar laminae as in typical ferns, while others possessed terminal sporangia borne on branchlets which probably were part of the frond.

Botryopteridaceae. The spore producing part of *Botryopteris* consisted of a massive aggregation of sporangia borne terminally in clusters on the ultimate branchlets of a much ramifying system (Fig. 33). The genus was apparently homosporous and produced this rather spectacular fructification somewhere on the frond. *Botryopteris globosa*, the best known form from the United States, had small, somewhat tear-drop shaped sporangia with an extensive apical annulus extending over the entire distal half of the sporangium (Fig. 30). A vertical zone of narrow cells marks the area of dehiscence. The sporangium wall consists of a single outer layer of relatively thick-walled cells, and a single inner layer of thin-walled cells. Reports in the literature suggest that in some cases the inner layer may have been absent in mature sporangia.

In their size and wall histology the sporangia of *Botryopteris* resemble those of leptosporangiate ferns more closely than those of any other coenopterid fertile part that is now known. Reduction of the annulus to fewer cells at the most distal part of the sporangium would result in a condition such as occurs in the family Schizaeaceae. On the other hand, reduction in annulus area and its confinement to one side of the sporangium would result in a sporangium of the type found in the family Osmundaceae. The overall structure of the fructification and terminal position of the sporangia on branchlets is totally unlike anything found among living leptosporangiate ferns.

Anachoropteridaceae. In 1916, Kubart described a specimen referable to *Anachoropteris pulchra* that consisted of a portion of a frond bearing parts of a type which had been described by Corda in 1845 under the name of *Chorionopteris gleichenioides*. Pinnules having pinnatifid laminae bore spore-producing structures attached along the margins that were so reflexed that the synangia lay on the lower surface of the leaf (Fig. 31). These spore-producing parts are synangia, each of which is composed of a group

of four sporangia fused basally and surrounded by a common outer wall of sterile tissue several cell layers thick (Fig. 32). Individual sporangia lacked annuli and produced large numbers of spores. This fructification is amazingly similar to several Carboniferous types of fertile parts having affinities with the Psaroniaceae. These fertile parts assigned to the Anachoropteridaceae are quite distinct from those of the other families of coenopterids, although the genus *Corynepteris*, which is referred to the Zygopteridaceae, shows the presence of a similar tendency involving the development of synangia on foliar areas. The structure of the individual sporangia is quite different in the two families, and those of the zygopterid genus are not surrounded by a wall of sterile tissue.

Discussion. It is clear from the foregoing descriptions that very few coenopterids are completely known, and of those few that are known rather completely, none serves as an adequate ancestral form for any major group of living ferns.

The plant body of the Stauropteridaceae is not highly differentiated and is extremely primitive in terms of leaf evolution. In addition, the stelar form does not suggest a condition that might have been ancestral to any living protostelic ferns such as those in the Gleicheniaceae, Hymenophyllaceae, or Schizaeaceae. The presence of heterospory in *S. burntislandica*, which is otherwise an extremely primitive vascular plant, suggests that the origin of heterospory (and possibly of seeds) need not have been correlated with a development of vegetative complexity in the course of plant evolution.

Of the members of the Zygopteridaceae, the clepsydrid forms resemble living ferns more closely than the etapterids, in regard to both the structure of the frond and the vascular pitting. It seems unlikely that any of the forms in the family having elaborate leaves could have served as ancestors of the more primitive families of living ferns in which the leaves are more generalized. The forms of stems and plant habits of the majority of zygopterid species are essentially comparable to those of various living ferns.

The fertile parts of the zygopterids show a certain degree of specialization, especially with respect to the characteristic band-shaped vertical annuli of the sporangia. It is unlikely that this type of sporangium represents an ancestral form of those in living leptosporangiate ferns, although it approaches them in having sporangial walls one cell layer thick. This reduction of the sporangial walls also rules out the possibility that the zygopterids were ancestral to eusporangiate ferns, such as the Ophioglossaceae or Marattiales.

Although the rather generalized vegetative structure of *Botryopteris*

might lead to its being suggested as a possible ancestral form for some living ferns, several features of the genus are against such an interpretation. Firstly, the vascular pitting is of a more advanced type than is found in most living ferns. Secondly, the complex fructification of the genus is unique and is not easily interpreted as a primitive stage in the evolution of any modern fern group. The sporangia suggest that the genus might have been a leptosporangiate fern, of a type no longer in existence. In this respect, Mamay has suggested (1957) that two lines of leptosporangiate ferns have evolved: one group having sporangia on the planated foliar areas of the frond, and one having sporangia on a very primitive frond and located terminally on stem-like axes. Living leptosporangiates would be included in the former group, and *Botryopteris* (and possibly *Biscalitheca*) would be an example of the second group, of which there are no living forms.

Among the Anachoropteridaceae, the genus *Grammatopteris* shows similarities to early forms of the Osmundaceae, and it may be argued that the genus should be assigned to that group rather than to the Coenopteridales. Until the frond and fertile parts of the genus are found the question of its relationships cannot be answered.

The genus *Anachoropteris* resembles the Marattiales in the organization of its fertile parts. However, its vegetative structure is different from that of the earliest known members of that order. When one considers the occurrence of synangia in the genus *Corynepteris* of the Zygopteridaceae, in the Anachoropteridaceae, and in the Psaroniaceae and Marattiaceae, it would appear that the tendency for aggregation and fusion of sporangia (of very different types in some cases) had been present in several groups of ferns. This also suggests that the marattialean type of fertile structure might be the result of parallel evolution and may not indicate natural relationships as clearly as has been supposed.

At present it is best to regard the forms included in the Coenopteridales as representing several groups of ferns (possibly several natural orders), all of which are extinct, and not having been ancestral to any living ferns. Like any group of plants, the coenopterids retained certain primitive features, such as the three dimensional branching of axes incorporated into the frond and sporangia borne terminally on branchlets. Other new features and specializations arose in the group, such as the various types of vascular pitting, the often highly elaborate vascular configurations in some frond axes, the planated and webbed megaphyll, and the development of several types of sporangia and sporangial groupings which at times were located on the lower surface of foliar areas. Our knowledge of the coeno-

pterids is still very incomplete, and only when it becomes much more thorough will we be able to establish more firmly the natural relationships of various forms in the order both to one another, and to various groups of living ferns.

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Mesozoic and Tertiary fern evolution and distribution

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The fossil record shows that when the Paleozoic era came to a close the initial stages in fern evolution had passed, and in those rocks formed during early Mesozoic time ferns can be recognized with essentially the same ease and assurance as in those that were formed much later. Consequently, the problems that confront the Mesozoic pteridologist may be quite different from those with which his colleagues of the Paleozoic must deal. For example, such questions as how the very early ferns are to be distinguished from other fossil vascular cryptogams that do not seem to belong to established classes, or whether such categories as the Coenopteridales should be regarded as ferns, are to him largely academic. Whether ferns came from psilophytes or whether psilophytes might have come from ferns is not particularly pertinent to one studying the ferns of later periods. Nature had settled that matter some 50 million years before ferns began to grace the Mesozoic landscapes.

The earliest Mesozoic ferns had evolved from Paleozoic ancestors, as did the other plants of that time. However, the trends in fern evolution during the transition from one period to the other are not well known. There is substantial evidence that 4 modern fern families, Osmundaceae, Marattiaceae, Schizaeaceae, and Gleicheniaceae, did originate during the Paleozoic era and have been in existence ever since, but most of the Paleozoic fernlike plants failed to survive the adverse climate of the Permian period, and new ones came into existence during the early stages of the Triassic period that followed.

In addition to the 4 families referred to that seem to have been in existence during the latter part of the Paleozoic era, there are 7 others that have fossil records that extend backward through the Tertiary period, and some of them can be traced into the early Mesozoic. These are Matoniaceae, Dipteridaceae, Cyatheaceae, Dicksoniaceae, Polypodiaceae, Salviniaceae, and Marsileaceae. These 11 families also embrace the majority of living ferns. The extent to which these families occur as fossils differs widely. Some are known from all of the periods; others have but single occurrences.

Osmundaceae. The Osmundaceae unquestionably have the most exten-

sive fossil history of any family of ferns. Their origin is still unknown, though the Early Permian *Grammatopteris*, one of the Coenopteridales, is believed to show some evidence of affinity with them. In the Late Permian there are some half dozen stem types (*Thamnopteris*, *Zalesskya*, etc.) that show definite osmundaceous features (Kidston and Gwynne-Vaughan, 1908-1914). All of these are protostelic, though in some the interior xylem is considerably modified, probably for water storage. Each stem was ensheathed by a layer of persistent leaf bases that contain vascular strands typical of the family.

In the Late Triassic *Itopsidema* (Daugherty, 1960) there is a well developed pith. The lack of leaf gaps, however, in this stem indicates an intrastelar origin of the pith. *Osmundites walkeri*, which is of the same age, does contain leaf gaps (Daugherty, 1941). In the Jurassic *O. dunlopi* the pith is enclosed by a partially broken xylem cylinder. In some respects this form appears intermediate between *Osmunda* and *Todea*. Thus from the Late Permian to the Jurassic both siphonostely and foliar gaps had developed in the osmundaceous stem.

Unless sporangia are preserved, foliage of the Mesozoic Osmundaceae is usually difficult to recognize with certainty. *Todites*, which resembles *Todea*, is an abundant genus in the Yorkshire Jurassic flora. Some species of the form-genus *Cladophlebis*, which occurs widely throughout the Mesozoic, certainly belong to the Osmundaceae.

Active evolution continued within the Osmundaceae throughout the latter half of the Mesozoic era and into the early part of the Tertiary period. The family also became widely distributed, and maximum size of individuals was achieved. *Osmundites carnieri*, from Paraguay, had a stem 9 cm in diameter with a stele 3.5 cm that contained at least 35 well separated xylem strands.

In the Wealden age (Lower Cretaceous) *Osmundites kolbei*, from Cape Colony, the xylem cylinder had about 56 partly confluent xylem strands. They, along with considerable tracheary tissue in the pith, represent the retention of a primitive character. From the Lower Cretaceous of Queen Charlotte Islands, off the western coast of Canada, comes *Osmundites skidegatensis*, which is in some respects the most remarkable member of the Osmundaceae. In its stem the departing traces interrupt the whole vascular cylinder, not only the xylem, and the external and internal phloem layers are continuous through the leaf gaps. Its stele is also a large one with about 50 strands. It is remote from any living *Osmundaceae* and probably represents an extinct branch of the family.

Remains of the Osmundaceae are either rare or have not been found in

Upper Cretaceous rocks, but they reappear in the Lower Tertiary. Numerous silicified stems of *Osmundites* that have weathered out of the Lower Tertiary Fort Union formation can be collected in the freshly cultivated wheat fields of North Dakota. The Eocene rocks, however, have yielded the greater share of the Tertiary specimens. *Osmundites dowkeri* is a well known species from the London Clay which is similar to *O. chandleri* from the Clarno formation of Oregon (Arnold, 1952). A Miocene or early Pliocene species is *O. schemnitzensis*, from Hungary. Except for the resemblance of *O. spetsbergensis* to *Osmunda regalis*, none of the Tertiary or older forms of *Osmundites* bear a very close resemblance to living forms, and none of the latter have significant fossil records, except possibly for spores in Pleistocene peat.

This somewhat extended treatment of fossil Osmundaceae seems justified because of the abundance of material that has been available and the well preserved structure shown by much of it.

Marattiaceae. This family is represented in the Late Paleozoic by certain fructifications that bear such names as *Asterotheca*, *Scolecopteris*, *Cyathotrachus*, etc., all household words among paleobotanists who have pulled plastic peels from coal balls. These have been compared by various authors with the fructifications of *Christensenia* and other members of the Marattiaceae. The Pennsylvanian and Permian age tree fern, *Psaronius*, may be an ancient member of the marattiaceous complex. Fertile fronds have not been found attached to its stems, and because of the distinctive structure of the stems, *Psaronius* is usually assigned to its own family, the Psaroniaceae.

A significant fact in connection with the Mesozoic history of the Marattiaceae is the wide distribution of its remains in the Arctic, although it is a tropical family at present. From the Late Triassic (Rhaetic) of Greenland Professor Harris (1931) has described fertile foliage under the name of *Marattiopsis* which he says differs from *Marattia* only in age. Other fertile material from the Triassic superficially resembles *Danaea*, and has been called *Danaeopsis*. It has sori of separate sporangia that are more like those of *Angiopteris* than *Danaea*, hence it is believed to be more closely related to the former genus than to the latter. Thus *Danaeopsis* may be a Triassic forerunner of *Angiopteris* rather than of *Danaea*. According to the late Professor A. C. Seward, the family Marattiaceae reached its developmental climax before Cretaceous time (Seward, 1922).

Schizaeaceae. The Carboniferous fructification *Senftenbergia* shows affinity with the Shizaeaceae, a resemblance that was noted by Corda when he named it in 1845. Though recent research has tended to confirm the

Paleozoic origin of the Schizaeaceae, the family shows no evidence of having made much headway until Jurassic time when *Klukia*, a genus with *Pecopteris*-type foliage became fairly abundant. *Lygodium* and *Anemia* are both recorded from the Jurassic. *Lygodium* shows worldwide distribution in the Eocene. Professor Henry Andrews has described interesting remains of *Anemia* from the Upper Cretaceous Frontier formation of Wyoming (Andrews & Pearsall, 1941). Fertile and vegetative parts that are almost identical with those of the living *A. adiantifolia* occur together, though not still in actual organic connection.

Gleicheniaceae. Although also believed to have arisen during the Paleozoic era, as indicated by the Pennsylvanian age fructification *Oligocarpia*, the Gleicheniaceae are believed to have "lain low" during the Triassic and Jurassic periods. They are not conspicuous ferns in any flora below the Cretaceous. The Mesozoic distribution of the family is from Greenland to Argentina.

The name *Gleichenites* was widely used by the older paleobotanists for forked fronds from Late Paleozoic and Mesozoic rocks. Some may represent the Gleicheniaceae, but most of them are of doubtful affinities. *Gleichenites coloradensis*, from the Upper Cretaceous Frontier formation, does bear considerable resemblance to certain living species of the family.

Gleicheniopsis, from the Upper Cretaceous Atane series of western Greenland, differs from *Gleichenia* in having sori with numerous small sporangia that contain relatively few spores (Tutin, 1932). Its three species, however, form a series that intergrades with *Gleichenia*, so the living and fossil forms may merely represent an expanded genus.

Matoniaceae. This family and those that follow have not been recognized in rocks older than Mesozoic.

Though the Matoniaceae have but one living genus (*Matonia*) 4 genera are recognizable in the Mesozoic (Hirmer & Hoerhammer, 1936). The oldest and the largest is *Phlebopteris* (*Laccopteris* of older literature). It ranges from Upper Triassic to Upper Cretaceous. Altogether there are about 7 named and well defined species, 3 of which come from western North America (Arnold, 1956). Two, *Phlebopteris smithii* and *P. utensis*, come from the Upper Triassic Chinle formation, and the other, *P. gallegi*, is from the Dakota sandstone. The other three genera, *Selenocarpus*, *Matonidium*, and *Matoniella*, are monotypic, and range from the Lower Jurassic to the Lower Cretaceous. The three genera are separated from each other on soral and indusial characters.

Dipteridaceae. This family has a notable fossil record in the Triassic and Jurassic (Ôishi & Yamasita, 1936). The fronds of the Mesozoic

dipterids are distinctly two-parted, as in the living *Dipteris*. In three fossil genera, *Dictyophyllum*, *Clathropteris*, and *Camptopteris*, the frond parting involves bifurcation at the apex of the petiole with subsequent development of a row of pinnae on the outer flank of each arm, apparently the result of twisting.

The Dipteridaceae and Matoniaceae show remarkably similar distributional patterns both during the past and in the present. Both families show worldwide distribution during the early and middle parts of the Mesozoic era, and restriction to a small area in the Old World tropics at present. The fossil record favors a close relationship between the two families, a subject on which there is disagreement when only the living forms are considered.

Polypodiaceae. The history of this family of ferns is in a nebulous state, which merely reflects the confused taxonomic status of many living members of the family. Many of its members are probably late products of evolution, the living bracken being an outstanding example. This cosmopolitan fern is virtually without a fossil record. Many of the unclassified ferns of the Mesozoic are undoubtedly polypodiaceous. The literature, however, does contain references to many genera usually placed in the Polypodiaceae, a few being *Davallia* (Early Jurassic), *Adiantum* (Jurassic), and *Asplenium* and *Onoclea* (Cretaceous). *Blechnum*, *Aspidium*, *Dryopteris*, *Pteris*, *Woodsia*, and *Woodwardia* have all been reported from the Tertiary. Our knowledge of the fossil occurrences of these genera is far from exact because most of the determinations were based upon vegetative foliage.

The polypodiaceous genus *Acrostichum*, which grows in recent tropical mangrove swamps, is rather rare in fossil floras. Abundant remains of it, however, have been found in plant-bearing chert in the Eocene age Green River and Clarno formations.

Dicksoniaceae. This is the largest family of ferns in the Middle Jurassic Yorkshire flora (Harris, 1961). It is represented there by *Coniopteris* with 5 species, *Kylikipteris* with 1 species, *Eboracca* with 1 species, and *Dicksonia* with 2 species. *Coniopteris* is widely spread in the Jurassic and Lower Cretaceous, but the remains usually consist of vegetative foliage which renders affinities with the Dicksoniaceae uncertain.

Cyatheaceae. Mention of the Dicksoniaceae leads to the Cyatheaceae, with which the Dicksoniaceae are often merged or treated as a subfamily. Most of our knowledge of the fossil Cyatheaceae is based upon petrifactions and casts of stems. Casts showing cyatheaceous type leaf scars are often assigned to *Protopteris*. Little fossil cyatheaceous foliage is known, hence soral characters, which are depended upon mostly in taxonomic treatment

of living members of the family, are unobservable. The family, however, definitely goes back to the Jurassic. *Protocyathea*, *Cyathocaulis*, and *Cebotiocaulis* are all genera based upon silicified stems and leaf stalks found in the Late Jurassic and Early Cretaceous of India and Japan respectively (Ogura, 1927). All of these forms show typical cyatheaceous steles which are broken by large leaf gaps, and characteristic leaf scars on the stem surface.

Some remarkable fossil cyatheaceous stems, from the Eocene of Texas, have been described as *Cyathodendron*. This genus represents a somewhat generalized form of fern that combines some of the characters of *Cyathea*, *Thyrsopteris*, and *Dicksonia* (Arnold, 1945).

Salviniaceae. It is not at all surprising to find the water ferns, *Salvinia* and *Azolla*, in the fossil state. We might expect them to occur more frequently than they actually do, as they grow in an environment that is prefabricated for fossilization. The floating leaves of *Salvinia* occur in very early Tertiary rocks (Florin, 1919), but the megaspores have been reported from the Late Cretaceous.

In at least three well known paleobotanical textbooks published during the last 20 years one reads that *Azolla* is not known in the fossil condition, though well preserved remains of this enigmatic plant have been known for a long time. The oldest azollas come from the Dutch Paleocene. The most remarkable of the fossil members is *A. intertrappeana*, described by an associate of the late Professor Birbal Sahni from the Intertrappean series of the Deccan Plateau in India. The silicified remains show megaspores with attached floats, and caught in the fibrils of the spore coats are microspore massulae bearing glochidia (Sahni, 1941). *Azolla primaeva* is a well preserved form from the Early Tertiary Princeton coal field in British Columbia.

Marsileaceae. I am not certain of any references to *Marsilea* in paleobotanical literature, but as I have seen the megaspores in Eocene chert, I include the family among those with fossil members.

Tempskyaceae. I said that there are a number of fossilized ferns that are not assignable to known families. Most of these are represented by compressed vegetative foliage. A rather striking exception is *Tempskya*, known from silicified trunks some of which are a foot in diameter (Andrews & Kern, 1947; Arnold, 1945; Read & Brown, 1937). *Tempskya* has been found to range widely throughout western North America. It seems to occur mostly in the middle portions of the Cretaceous sequence, though it may possibly extend as far down as the topmost Jurassic. The greatest number of specimens are found in Montana, Oregon, Idaho, and Colorado,

but they occur elsewhere. For a long time they were mistaken for palm trunks, hence they escaped recognition. The trunks are made up of large numbers of intertwined stems of small diameter that are held together by a matrix of adventitious roots. We know nothing of the foliage or fructifications of this monstrosity, and the internal structure, though often very well preserved, has been of little help in deciding upon the affinities of the plant.

The old custom of adding the suffix "*-ites*" to modern generic names and using them for fossils has led to erroneous ideas of the geologic history of many fern genera. Familiar examples are *Adiantites* and *Hymenophyllites*. *Adiantites* has been used for fossil ferns from the Devonian to Recent, and it means nothing concerning the history of the family. *Hymenophyllites* has been used indiscriminately for almost any kind of fossil fernlike plant with finely divided foliage, but it shows nothing of the history of the Hymenophyllaceae.

Conclusions. Mesozoic and Tertiary ferns provide excellent material for rewarding research. Fossil ferns have definite advantages over seed plants because their fructifications are more often found connected to vegetative parts. With modern techniques well preserved fern compressions may be studied and interpreted with precision approaching that used for living ferns. New forms and better preserved material of already known forms continue to be found. However, we need not await newly discovered material to learn more about ancient ferns because much could be accomplished by merely going through museum collections and sorting out specimens that had never been thoroughly studied or had been only casually examined and then forgotten. Then there is considerable information in the older literature, especially in obscure and not readily accessible publications, that has been generally overlooked and was never organized and assimilated into the more comprehensive works on paleobotany.

Morphologists are sometimes prone to blame the imperfections of the fossil record for the difficulties in interpreting vascular plant phylogeny. Paleobotanists of course do not need to be reminded of this, but the difficulties stem just as much from a lack of more knowledge of living plants. Morphological concepts are built too much around a "typical plant," without any very concrete idea of what a typical plant is. To qualify as a plant morphologist one must be able to recite from memory the life history of a moss (which moss is never specified), a fern (any fern or no particular fern will do), a cycad (*Zamia*, the most advanced one of course), and if any time remains, pine and lily. This series makes up the ritual of conventional plant morphology.

A particularly serious handicap in understanding Mesozoic and Tertiary ferns is our rather severely limited knowledge of the structure of the leaf stalks and rhizomes of living ferns. Of this, the Osmundaceae furnish an excellent case in point. In this family a fine series of well preserved stems is known that range from the Late Paleozoic almost to the Recent. But we have extended knowledge of the anatomy of only three of the dozen or more living *Osmunda* species, and of these a number of structural details have never been fully elucidated. Our knowledge of the anatomy of fossil Osmundaceae probably exceeds that of the living members. What the extinct forms led to, and how the living ones are related to them must remain unknown until more is learned of the latter. With any group of ferns it is impossible to take full advantage of what we know of the fossil forms when we are so ignorant of living members.

Only when we can compare the extinct with the living types can we determine phylogenetic lines with any degree of finality. To be usable in this respect taxonomic descriptions of ferns should be accompanied by illustrations of at least the grosser structural features of the leaf stalks and rhizomes. One suspects that such information might ultimately find use in the taxonomy of living ferns as well if more of it were available.

An observation of a different nature is that the ferns have been moderately successful in their struggle for existence in the biological world. They have been, in fact, the most successful of all spore-bearing vascular plants. They did, along with other groups, suffer a major setback by the ravages of an adverse Permian climate, but they sprang back to life again at the first opportunity, which came during the Triassic. They were not killed off during the Cretaceous period by the rising angiosperm tide as were the cycadeoids, many of the true cycads, and most of the Ginkgoales, and at the present moment they seem to be holding their own, stubbornly refusing to go over the brink into oblivion. The dire prediction made several years ago by Professor C. J. Chamberlain that the cycads will be extinct in the next geological age cannot be applied to the ferns. They will survive the present epoch, and probably the next one. Beyond that, I do not predict.

The picture sometimes presented to us of Jurassic floras laden with ferns are probably somewhat overdrawn. It happens that certain Jurassic floras are better preserved than others, and we know more about the plants in them. Much of our concept of Mesozoic vegetation is based upon the large and exceptionally well preserved Jurassic Yorkshire flora, which happens to be what is probably the best assemblage of fossil plants anywhere in the world. This flora also contains a large number of ferns.

Maps that purport to show the distribution of Mesozoic ferns depict

many of the families and genera ranging far beyond their present limits. Of special interest is the apparent past ranges of such present day tropical families as the Gleicheniaceae, the Marattiaceae, and the Matoniaceae into Arctic regions (Harris, 1931; Hirmer & Hoerhammer, 1936; Seward, 1922, 1926). At times during the past members of these families could have tolerated colder climates than the survivors do at present, but the possibilities of the continents having drifted or that the poles have shifted greatly complicates problems of past distribution of ferns. Maps that show the past distributions of fossil ferns are inconclusive at best.

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Correlation of fern tracheid morphology and evolutionary divergence

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Studies of the xylem have been one of the chief sources of information regarding trends of diversification in the higher groups of vascular plants. The work of Bailey and Tupper (1918), Frost (1930a, b), Cheadle (1943) and others has resulted in the determination of evolutionary trends of specialization in the tracheary elements of gymnosperms and angiosperms which are well known to plant morphologists. Among these are the following: (1) the long tracheary element is primitive, the short one advanced; (2) scalariform pitting is primitive, opposite pitting intermediate, and alternate pitting advanced; (3) the tracheid is primitive, whereas the vessel member, derived from the tracheid, advanced.

With these points in mind, I undertook a broad survey of the morphology of fern tracheids (White, 1963a,b) to determine whether or not there are any trends in the morphology of the metaxylem tracheids of ferns and whether these are similar to those described for the secondary xylem of angiosperms. The survey included 210 species of ferns representing 90 genera and 18 families (after Copeland, 1947).

Cell length. Measurements were made of the lengths of 100 tracheids each from the rhizome, root and petiole of each species. The average lengths and standard deviations were computed. From a casual review of the averages obtained, it was not immediately apparent that there was any pattern of tracheid length change with evolutionary divergence. A statistical study was then made in order to determine whether there was any correlation between evolutionary level and average tracheid length.

In order to accomplish this, a quantitative technique was needed to express evolutionary divergence. Certain characters which are generally acknowledged to be of systematic importance in the ferns were used as the basis for the development of a scale of divergence. These have been described fully by Wagner (1954), and of the 10 he described, eight were used in this study: (1) habitat, (2) spore morphology, (3) gametophyte, (4) gametangia, (5) venation, (6) dermal appendages, (7) sporangia and (8) soral maturation. On the basis of these characters a total divergence index was developed for each family of ferns. This was estimated by giving one point to a family for each advanced character and a half point

when a character was intermediate between advanced and primitive. No points were given if the primitive state of the character was general for the family. It was thereby possible to ascribe to each family an "index number." This scale ranges from advanced families such as Polypodiaceae, Vittariaceae, Marsileaceae and Salvineaceae with index numbers of 6 and 7 to the primitive families Marattiaceae, Ophioglossaceae, Gleicheniaceae and Osmundaceae with index number of 0, 1, 1.5 and 2 respectively.

With both figures, the average length of the tracheids and the index number, it was possible to compute a Pearson's Correlation Coefficient (Dixon and Massey, 1957). This test measured the extent of relationship between the degree of relative divergence and average tracheid length. In doing this, the index number was applied to the family, genus and species levels thus increasing in that order the number of observations.

There was a significant correlation between root tracheid length and divergence ($-0.52 < r < -0.12$ for genera: $-0.37 < r < -0.04$ for species) at the 5% level. Such a correlation was not found for either the rhizome or petiole. A correlation coefficient as large in absolute value as that found for the roots would occur by chance only 5 times in 100. Although there is a tendency in both of the other organs in the direction of correlation between the two factors, it was never significant to the 5 percent level.

Admittedly, the parameters are very general and it is hoped they will be refined in subsequent work as more information becomes available. Numerous factors including location of tracheids in the plant, ecology of the plant, age of the plant, and chromosome number were found to affect tracheid lengths. As many of these variables as possible were made equivalent, but the great variation which remained in the measurements indicates a need for the further improvement of the procedure by which tracheids were chosen for measurement. With all these difficulties, and the large number of families at the same index level (8 of the 18 families were at levels between 5 and 6), the fact that there was a correlation in the root, and tendencies in the direction of positive correlation in the other organs seems important to me.

The correlation found between root tracheid length and taxonomic divergence is not merely a statistical one. In general, the primitive families *do* have longer tracheids than the advanced ones: Hymenophyllaceae (3.3 mm), Gleicheniaceae (4.7 mm), Schizaeaceae (3.1), and Osmundaceae (3.0 mm), contrasted with advanced families such as Grammitidaceae (1.8 mm), Polypodiaceae (1.8 mm) and Vittariaceae (1.4 mm). Examples of two important families which do not fit this pattern are the Ophioglossaceae (1.7 mm), a primitive family with short tracheids, and the Marsileaceae

(3.1 mm), an advanced family with long tracheary cells. *Within* families, there is also support for the correlation: In the Marattiaceae, Schizaeaceae, Gleicheniaceae and Aspidiaceae, long tracheids are found to occur in species with anastomosing veins (another primitive character). In the Aspleniaceae and Pteridaceae genera considered the most primitive on the basis of other characters, have the longest tracheids. There are also exceptions to this correlation in such families as Ophioglossaceae, Hymenophyllaceae, Cyatheaceae, and Marsileaceae. With regard to these exceptions, it is necessary to remember that in the ferns we are dealing with three lines of evolution: the Ophioglossales, Marattiales and Filicales, and that in the last there are some families which have become very highly specialized (i.e. Marsileaceae, Salviniaceae).

Pitting patterns. Pitting patterns on the lateral walls of tracheids also show some variation when tracheids of species of low index level are compared with those of higher index number. Scalariform lateral pitting is recognized as the most common type in the metaxylem of ferns, but there are two exceptions to this: the Ophioglossales and Marattiales have species with circular bordered pits.

A survey was made of the pitting patterns present (scalariform alternate and opposite) on samples of 50 tracheids from each organ. The percentage occurrence of each pattern was noted and the results were charted against families arranged according to their divergence index number. Three main points emerged from this survey:

(1) Although scalariform pitting is present in nearly every family (in general it is the sole pattern in the most primitive families), it is the predominant pattern in most families except the most advanced. In these advanced families alternate and opposite patterns, rather than the scalariform pattern, are the rule.

(2) When the survey is broken down according to the organ from which the tracheids were chosen a pattern emerges. The tracheids in the rhizome are typically scalariform in all families except the most advanced, while the lateral patterns of alternately and oppositely arranged pits are most common in petiolar tracheids. An intermediate condition between that of the rhizome and the petiole is found in the root.

(3) In the root tracheids of species with the most highly modified lateral pitting, the overlap area between contiguous tracheids is more specialized than that usually associated with the "typical" fern tracheid.

From the families of low relative divergence index number to those of higher rank, there is a decrease in the percentage of occurrence of the typi-

cal scalariform pitting pattern, and a concomitant increase in the occurrence of pits which are of opposite and alternate arrangement. In some cases, the pits approach the circular bordered condition.

Associated with this change in lateral wall pattern is the occurrence of distinct overlap areas between contiguous tracheids. The portion of the tracheid which overlaps in a file tends to maintain the scalariform pitting pattern, whereas the lateral walls in the tracheids may have a modified pattern. This combination results in tracheids which frequently appear very similar to vessel members.

Vessels and vessel-like cells. Two major characters differentiate vessel members from typical tracheids: (1) the presence of a distinct end-plate (area of overlap between contiguous cells in a file), and (2) the end plate of vessel members are perforated, in contrast to the presence of primary walls and middle lamella in the pits of typical tracheids. The first condition is a necessary prerequisite to the second—this was pointed out by Frost in 1930 (1930a, b). It is therefore possible to consider tracheids with end plates (specialized overlap areas) as intermediate between typical tracheids and typical vessel members. As noted previously, there is an increase in the occurrence of "end plates" among families of intermediate to higher index number. They are of most frequent occurrence in root tracheids, less frequent in the petiole, and are virtually absent in the rhizome. Such end plates were not observed to occur in any family with an index number lower than 4.5, and occurred to some extent in every tracheid in the families Grammitidaceae and Vittariaceae. Thus with an increase in index number, there is a general percentage increase in the occurrence of tracheids with specialized overlap areas.

The single, most important characteristic of a vessel member is the perforation plate. Early in this survey (White, 1961), elements were found in the root of *Marsilea quadrifolia*, which were determined to be vessel members by the passage of India ink particles through several contiguous cells. The only other known occurrence of this cell type among the ferns is in *Pteridium*. After the discovery of vessels in the root of *Marsilea* (several other species in the genus have now been shown to have vessel members), species of *Pilularia* and *Regnellidium*, presumed to be closely related to *Marsilea*, were examined. In all cases, only typical tracheids were found.

In *Marsilea and Pteridium*, an additional character was noted which distinguishes the pits on the end plates from those of the lateral walls. The pits of the end walls are generally larger, and the width of the secondary thickenings, when present, are much reduced in contrast to those on the lateral walls. A careful survey of pit sizes in tracheids of all three organs

of representative species of each family resulted in the following conclusions: (1) There appears to be no correlation between pit size and relative evolutionary advancement in the ferns. The pits of advanced families such as Polypodiaceae and Vittariaceae are not much different from those of the primitive families Marattiaceae and Gleicheniaceae. Pit sizes appear to be variable within and between families of ferns and show no clear evolutionary trends. (2) The rhizome tracheids revealed the least difference in pit sizes between overlap areas and lateral areas. Those of the petiole were intermediate, while the most conspicuous differences between lateral and end-plate pit sizes were in the root tracheids. (3) In the entire survey, only two other species had characteristics which approached those found in *Pteridium* and *Marsilea*. In both cases these were root tracheary cells, and although sections have been inconclusive as yet, I am referring to these cells as "presumptive vessel members."

In both *Woodsia ilvensis* and *Notholaena sinuata* the xylem cells are short, have modified lateral pitting, have end plates which are short and more or less oblique, and the pit size on the end plate is large in proportion to the bar width. In tracheids of both species there appears to be a reduction in the number of bars of secondary thickening on the end plate with a decrease in the angle of the end plate. This last feature is more characteristic of *Woodsia* than of *Notholaena*.

In view of these discoveries, other species which have a dry habitat (in common with the species just described) were surveyed including 16 species of *Woodsia*, several of *Notholaena* and selected species of *Cheilanthes*, *Pellaea*, *Ceterach*. None had characters similar to those described. Hybrid *Woodsia* species tended to have the more general character of the tracheid rather than the specialized vessel-like character found in *W. ilvensis*. The vessel member character appears to be one which occurs more or less at random, but at least it is restricted to intermediate and advanced families and absent in families generally considered most primitive. It is thus considered a derived character.

In summary, the results of this study of tracheary cells of living ferns are as follows:

(1) Statistical analysis, though still far from exact, shows a correlation, significant at the 5 percent level in root tracheids, of relative divergence with decrease in average tracheid length. There are indications of a similar trend in the other organs, but the correlation was not significant.

(2) With an increase in taxonomic divergence there is also a percentage increase of occurrence of modifications of the scalariform pitting pattern: alternately arranged pits become more common as do oppositely arranged

pits. In some of the more specialized families, lateral wall pits are lacking altogether.

(3) Along with a decrease in length, and a percentage increase in occurrence of modified lateral pitting, there is also an increase in the occurrence of specialized overlap areas, or end plates. In one case, *Marsilea*, the occurrence of vessel members was proven. In two cases, *Woodsia ilvensis* and *Notholaena sinuata*, presumptive vessel members were described. This condition appears to be of random occurrence and at present I am unable to correlate it with anything common to all the species.

On the basis of the characters which have been described here as derived through evolution: shortness, modified lateral pitting and the occurrence of vessels, or presumptive vessels, the "original" primitive fern tracheid appears to be as already suspected: long, slender, tapered, and scalariformly pitted.

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Evolution in the leaf of living ferns

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There are two complementary approaches to the study of evolution of the fern leaf. One is the phyletic approach in which not only the leaves of living ferns but especially those of fossil ferns are considered. The phylogeny is based on the sequence of the leaves in the fossil record and on the interpretation of the relationships of different types of leaves. Although this approach has been frequently developed, the fossil record is so fragmentary in its scope that phyletic theory must be extensively employed to supplement the facts. Another approach is that of comprehensive study of the leaf of living ferns. Although this approach must also employ theory, it has the advantage that there are some nearly complete recent evolutionary lines and in these the relationships of species and characters are accordingly relatively certain. Also in recently evolved groups there will be few extinct species and the full scope of evolutionary diversity can be studied. Unfortunately we can not yet fully exploit this approach because of the few modern monographs from which evolutionary information may be obtained. However, there is much pertinent information available and I will utilize some of it to discuss fern leaf evolution in terms of a single topic—leaf form (leaf architecture) in the living Filicopsida (Filicinae of Christensen, 1938; Filicineae of Copeland, 1947).

The diversity of leaf form. There is much diversity in the leaf form of the Filicopsida. Among some nine thousand species at least several hundred different patterns can be distingnished. Most of these patterns, however, differ from related forms only in minor details. In order to discuss this diversity, I am classifying leaf form into six principal types. This classification is based on the arrangement of the primary parts of the lamina (pinnae, pinna-lobes, or their equivalent) and on the definite or indefinite growth of the lamina. This classification serves the present discussion but it is not intended for general use. The examples will augment the brief and somewhat general definitions of the forms. In the first five leaf forms, the lamina has definite growth and is determinate. In the sixth leaf form the lamina has continuous, indefinite growth and is indeterminate.

1. Pinnate-determinate. The lamina has pinnately arranged parts and the apex of the lamina usnally is fnlly expanded: *Adiantum pulveru-*

tentum (Fig. 1), *A. Lorentzii* (Fig. 8), *Pellaea sagittata* (Fig. 12), *Lindsaea bifida* (Fig. 24). Rarely there is a dormant meristem at the apex: *Danaea Moritziana* (some leaves), *Asplenium alatum*.

2. Simple-entire. The lamina is simple and not lobed or laciniate: *Adiantum reniforme* (Fig. 2), *Polypodium angustifolium* (Fig. 17), *Vittaria lineata* (Fig. 18), *Pyrrosia lanceolata* (Fig. 19).

3. Helicoid. The parts of the lamina are borne on only one side of the rachis branches: *Adiantum pedatum* (Fig. 3), *Matonia pectinata*, *Dipteris conjugata*, *Neocheiropteris palmatopedata*.

4. Radiate. The parts of the lamina radiate from one (or nearly one) point: *Cheilanthes (Adiantopsis) radiata* (Fig. 4), *Christensenia aesculifolia*, *Marsilea* species.

5. Furcate. The parts of the lamina branch in a dichtomous or subdichotomous manner. In some species the arrangement of the branches is flabellate: *Schizaea dichotoma* (Fig. 5), *Peltapteris peltata*, *Actinopteris australis*. In other species it is less regular: *Ophioglossum palmatum*, *O. pendulum*, *Platycerium bifurcatum*, *Phanerosorus sarmentosus*.

6. Pinnate-indeterminate. The lamina has indefinite growth; there is an actively growing meristem at the apex or some other portion; the parts are arranged in a pinnate manner: *Gleichenia* (Fig. 6), *Dicranopteris*, *Lygodium*, *Blechnum volubile* (Fig. 7).

A few forms are not readily accommodated in the above classification. They may be intermediate between two of the forms or they may combine two types of arrangement in a single leaf. One of these, mentioned below, is intermediate between the pinnate-determinate and the pinnate-indeterminate form. In this the apical meristem grows slowly and a bud is still present when the leaf dies; *Jamesonia canescens* (Fig. 21) and other species of the genus, *Eriosorus aureonitens* and *Polypodium sericiolanatum* are examples of this form. The minute bilobed leaves of *Azolla* are unique and have not been included in this classification.

Within each of these principal forms, there usually are a large number of variants differing in such characters as the relation of the parts of the lamina to each other in spacing and in the angle at which they are borne on an axis; the shape and size of the lamina and of its parts; and the relative size of the lamina and the petiole. For example, in *Adiantum*, minor variants of leaf form are illustrated by such species as *A. pulverulentum* (Fig. 1), *A. Lorentzii* (Fig. 8), *A. latifolium* (Fig. 9) and *A. digitatum* (Fig. 15).

Most of the species of the Filicopsida have the pinnate-determinate form; the simple-entire form is infrequent and all of the other forms are

rare. An estimate of the proportion of the species and genera that have the principal leaf forms follows. In making this estimate, I have assumed that each species has only one form (which is not always true). A genus is placed under each form that is represented by one of its species. Perhaps 1% of the species have a form intermediate between two of the principle forms.

Type 1, pinnate-determinate, 85% of species and genera.
Type 2, simple-entire, 10% of species and 17% of genera.
Type 3, helicoid, less than 1% of species and genera.
Type 4, radiate, less than 1% of species and genera.
Type 5, furcate, less than 1% of species and genera.
Type 6, pinnate-indeterminate, 2% of species and genera.

The occurrence of the different leaf forms in the families of the Filicopsida is shown in Table 1.

TABLE 1. *Percent of species with different leaf forms in the families of Filicopsida.*

Family, number of species	Pinnate-determinate	Simple-entire	Helicoid	Radiate	Furcate	Pinnate-indeterminate
Ophioglossaceae 80	38	60			2	
Marattiaceae 200	99	—1		—1		
Osmundaceae 20	100					
Schizaeaceae[1] 160	58	12			5	25
Marsileaceae[2] 70		9		90		
Salviniaceae[3] 16		62				
Gleicheniaceae 120	2					98
Matoniaceae 4			50		50	
Hymenophyllaceae 500	92	8				
Loxsomaceae 4	100					
Hymenophyllopsidaceae 3	100					
Plagiogyriaceae 30	100					
Dicksoniaceae 40	100					
Cyatheaceae 600	+99	—1				
Polypodiaceae 7000	86	13	—1	—1	—1	—1

[1] Classified according to the form of the sterile leaf.

[2] *Regnellidium* with a bilobed leaf is omitted.

[3] 38% of the species (the genus *Azolla*) have a minute bilobed leaf that has not been included among the principal forms.

The ecology of leaf form. An analysis of the relationship of leaf form to environment is complicated by the variety of leaf forms (the principal forms and their many minor variants) and by the variety of environments. In order to simplify the discussion and to bring out some of the important correlations with leaf form, the environments in which ferns grow have been grouped into five types. In estimating the number of species that grow in each environment, I have assumed that each one grows in only one environment (which is not always true). About 15% of the species of Filicopsida grow in subtropical and temperate environments which are intermediate between the ones discussed and these have not been included.

1. Tropical mesic. There is adequate moisture in the substrate all (or most) of the year, the atmosphere is relatively humid and the temperature is always well above 0°C. This is the optimal environment for ferns and 65% of the species grow within it. All of the principal leaf forms occur in this environment and there are many minor variants of them. Most of the species, however, have leaves with a relatively large amount of surface. The lamina may have broad surfaces, or may be decompound; frequently it is quite large (more than 1 m long). The texture of the lamina is relatively thin to moderately coriaceous, usually correlated with the atmospheric humidity. The leaves are usually persistent for at least a full year. Examples of species with this characteristic leaf form are: *Saccoloma domingense* (Fig. 10), *Adiantum pectinatum*, *Tectaria dilacerata*, *Dennstaedtia bipinnata*, *Hypolepis repens*, and *Lophosoria quadripinnata*.

The ferns with the pinnate-indeterminate form are most frequent in the tropical mesic environment although not confined to it. They are similar to the leaves mentioned above in having large amounts of leaf surface. The climbing leaves, best developed in *Lygodium* and *Blechnum volubile*, are able to occupy a niche in the vegetation different from that of other fern leaves. The scrambling leaves of *Gleichenia* and *Dicranopteris* may form thickets or may scramble over shrubs and small trees. They also tend to occupy a different ecological niche than those of other ferns.

2. Tropical xeric, terrestrial. There is adequate soil moisture only seasonally, although it may be augmented by local seepage and, in some areas, by dew; the atmosphere is relatively dry and the temperature is always well above 0°C. This environment includes the deserts and semideserts of the tropics; about 5% of the species of ferns grow within it. The leaves are predominantly of the pinnate-determinate form. There are many minor variants of this form but most of them have a lamina with a relatively small amount of leaf surface. The leaves are small and have either few, relatively broad segments or many small segments. The tex-

ture of the lamina is usually coriaceous. Examples of species with this characteristic leaf form are *Notholaena sinuata* (Fig. 11), *Pellaea sagittata* (Fig. 12), *P. ternifolia*, and *Cheilanthes myriophylla*. Among these xeric ferns, a similar leaf form has been developed in different genera, for example, in *Notholaena Standleyi* (Fig. 13) and *Pityrogramma triangularis* (Fig. 14); in *Notholaena parvifolia* and *Pellaea sagittata*; and in *Notholaena candida* and *Cheilanthes farinosa*. The leaves of most of the species in this environment are persistent for all or most of a year. They have the ability to become dormant during a brief dry period and then revive with precipitation. Their period of activity is accordingly extended beyond the duration of the principal wet season. The small amount of leaf surface seems to be an adaptation to the xeric season of the environment rather than to the mesic season.

There are a few species that have deciduous leaves that die as soon as adequate moisture is no longer available. These leaves are active only during the mesic season and they tend to have broad surfaces and a thin texture. In these characters they are more like the leaves of the tropical mesic environment than the leaves of the typical xeric species; their form is adapted to the mesic season of the environment rather than to the xeric season. *Cheilanthes Braudegei* and the closely related *C. fractifera* are examples of these species with deciduous leaves. On the coastal lomas of Peru, *Adiantum digitatum* (Fig. 15) affords another example.

3. Tropical xeric, epiphytic. There is adequate substrate moisture only seasonally, the atmosphere is relatively humid seasonally (sometimes it may be dry during the day and very humid at night), the temperature is always well above 0°C. This environment is found in tropical forests with a pronounced dry season (or seasons); about 10% of the species of ferns grow within it. Most of the species have the simple-entire leaf form although the pinnate-determinate form (usually represented by a deeply pinnatifid or pinnatisect lamina) is also common. In either case there is a small amount of leaf surface because of the small size and simple form of the leaves. The texture is usually coriaceous. Most of these leaves have the ability to become dormant when adequate moisture is not available and to revive when it is restored. The leaves are persistent for all or most of a year. The small amount of leaf surface seems to be an adaptation to the xeric season of the environment and perhaps to brief dry periods during the mesic season. Examples of species with this characteristic leaf form are: *Polypodium polypodioides* (Fig. 16), *P. angustifolium* (Fig. 17), *Vittaria lineata* (Fig. 18) and *Pyrrosia lanceolata* (Fig. 19). Species in

different genera often have essentially the same leaf form (compare, for example, Figs. 17 and 18).

The leaves of the tropical xeric epiphytic ferns have a simpler form than those of the tropical xeric terrestrial ferns. This may be related to the rather variable moisture supply during the growing season in the former environment and the more constant supply in the latter environment. The substrate in the epiphytic environment is limited in extent and is readily subject to desiccation. Even during the wet season desiccation may occur during brief dry periods or even during the day. The substrate in the terrestrial environment is usually extensive and will remain moist throughout the wet season.

A few species have leaves that are deciduous at the end of the wet season, at least in some parts of their range. Examples of these are: *Drynaria Fortunei* (Fig. 20), *Ophioglossum palmatum*, and *Anetium citrifolium*. These leaves, like those of the species with deciduous leaves among the tropical xeric terrestrial ferns, have relatively broad and large surfaces (although sometimes of a simple form) and the form seems adapted to the environment during the mesic rather than the xeric season.

4. Tropical alpine. The soil mixture is variable, the atmosphere is periodically dry and very moist, either diurnally or seasonally, and the temperature is near or below 0°C. during the night. This environment is of local occurrence in the tropics and is often poorly defined. Less than 1% of the species of ferns grow within it and most of these also grow in subalpine areas. It is of special interest because of the similar leaf form of *Jamesonia* (Fig. 21) and *Papuapteris* (Fig. 22)—genera that belong to different tribes of the Polypodiaceae. In these genera the lamina is linear, with numerous imbricate pinnae; in the former genus a bud is usually retained at the apex while in the latter the apex is fully expanded. *Jamesonia* occurs in the American Andes and has evolved from *Eriosorus* (Tryon, 1962) in which the leaves are usually fully expanded and pinnate-determinate. *Papuapteris linearis* grows in the mountains of New Guinea and has evolved from *Polystichum* in which the leaves are expanded and pinnate-determinate. A similar example, although the form is not as extreme, is found in two species of *Gleichenia*. *Gleichenia simplex* of the Andes and a form of *G. vulcanica* occurring in the mountains of New Guinea both have small, pinnate-determinate leaves. The latter species is represented at lower elevations by the branched lamina (pinnate-indeterminate form) characteristic of the genus.

5. Boreal and Arctic. The soil and atmospheric moisture are variable during the warm season, the temperature is seasonally well below 0°C.

About 5% of the species of ferns grow in the boreal and arctic environment. Nearly all of them have leaves of the pinnate-determinate form. In most of the species the leaves die at the end of the warm season, but in a few they are evergreen and the form of these is similar to that of the deciduous ones. The leaf form is adapted to the environment during the growing season. In mesic habitats the leaves are similar to those of the tropical mesic ferns, for example, in such species as *Dryopteris Goldiana* and *D. spinulosa* var. *americana* (Fig. 23). In xeric habitats the leaves are like those of the tropical xeric terrestrial ferns.

The truly aquatic ferns have not been mentioned in the previous discussion. Most of the genera grow, and have the same leaf form, in both tropical and boreal environments. In *Salvinia* the leaves are minute and simple-entire, in *Azolla* they are minute and bilobed, in *Pilularia* they are linear, in *Marsilea* they are radiate, and in *Regnellidium* bilobed. *Ceratopteris* has the floating leaves with an inflated petiole, pinnate-determinate in form. The leaf form in each of these genera is adapted to the aquatic environment.

The evolution of leaf form. A survey of the living ferns suggests that there have been two principal trends in the evolution of leaf form—the evolution of a simpler leaf form from a more complex one and the evolution of all of the other principal leaf forms from the pinnate-determinate form. Both trends may occur in the same evolutionary line, especially in the evolution of the simple-entire form.

Simplification of the leaf form in an evolutionary line is illustrated in the genera *Lindsaea* (Kramer, 1957), *Doryopteris* (Tryon, 1942, 1944), and *Anemia* (Mickel, 1962). In each of these genera, the primitive species (accepting the author's phyletic conclusions) have relatively complex pinnate-determinate leaves while one or more species with simple-entire, or few-lobed, leaves are advanced. *Doryopteris rufa*, *D. quinquelobata*, and *Anemia elegans* are species with few-lobed leaves. The most complete evolutionary line is found in *Lindsaea* where *L. bifida* (Fig. 24), with a tripinnate-pinnatifid lamina, is primitive; *L. lanceа* (Fig. 25), often with a bipinnate lamina, is more advanced; *L. Ulei* (Fig. 26), with a once pinnate lamina, is further advanced; and *L. reniformis* (Fig. 27) and *L. cyclophylla*, each with a simple-entire lamina, are most advanced. Other genera undoubtedly provide examples of the evolution of the simple-entire form from the pinnate-determinate one. In *Thelypteris*, *Adiantum*, *Danaea*, and *Cyathea* there are numerous species with the pinnate-determinate form and one, or very few, with the simple-entire form. The latter species are *Thelypteris gigantea*, *Adiantum reniforme* (Fig. 2), *Danaea*

simplicifolia, and *Cyathea sinuata*. Although the phyletic relationships of the species in these genera are not well known, one may assume that the species with the simple-entire form are advanced. There is no correlation of the simple-entire (or few lobed) leaf form with the environment in the species mentioned above; they grow in the tropical mesic environment along with species having more complex leaves.

Leaves of species of the tropical xeric epiphytic environment are commonly pinnatifid or entire and these also illustrate the evolution of simple leaves from more complex ones. The tropical xeric terrestrial ferns that have a reduced leaf form may also illustrate this trend. The simple, or relatively simple, leaf form is undoubtedly an adaptive feature developed during the evolution of these xeric species into their rather extreme environment. Through the course of the evolution of the Filicopsida, the tropical mesic environment probably has been the principle center of evolution and the source of the basic lines that have migrated into and developed in other environments. A comparative study of the relationships of xeric species with their mesic ancestors, that might establish the kind of leaf form from which the xeric species evolved, would be of much interest.

The second evolutionary trend is from the pinnate-determinate form to one of the other principal forms. This has been sufficiently discussed for the simple-entire form. The helicoid form as represented in the leaf of *Adiantum pedatum* (Fig. 3) is rare in the genus. Nearly all of the many species of *Adiantum* have the pinnate-determinate form and the helicoid form does not occur in related genera. In this species of *Adiantum*, the helicoid leaf appears to have been derived from an ancestral pinnate-determinate leaf. The evolution of the radiate form from the pinnate-determinate is illustrated in the genus *Christensenia* of the Marattiaceae. Mamay (1950) considers this genus to be the most advanced in the family on the basis of several derived characters such as the areolate venation and the type of sorus. It also appears that the radiate leaf is a derived character. The other species of the family have the pinnate-determinate form or very rarely the simple-entire form. Species of the Polypodiaceae with the furcate form, such as *Peltapteris peltata*, *Actinopteris australis*, and *Platycerium bifurcatum*, occur in relatively advanced genera of the family. The furcate leaf in these genera would represent a derived rather than a primitive condition. These and other species with furcate leaves have been considered by Wagner (1952) to have been derived from ancestors with typical pinnate leaves. The scrambling pinnate-indeterminate leaf is best developed in *Gleichenia* and *Dicranopteris* (Gleicheniaceae). In his study

of these genera, Holttum (1957) considers their leaves to have evolved from a *Cyathea*-like (pinnate-determinate) leaf. Among other evidence, he cites the typical pinnate leaves that are developed in young plants of *Gleichenia glauca*, a species that he considers to be primitive in the genus on the basis of other characters. The climbing pinnate-indeterminate leaf of *Blechnum (Salpichlaena) volubile* (Polypodiaceae) has also undoubtedly been evolved from a pinnate-determinate ancestor. Its leaf is unique in the family and hardly can be considered as primitive.

Conclusion. There is convincing evidence among living ferns that the pinnate-determinate leaf form has evolved into all of the other principal forms, and on this basis I consider it to be the primitive type of the living Filicopsida. There have been two adaptive evolutionary developments from the pinnate-determinate leaf that are of special importance. One is the simplification of the lamina and reduction of its surface (finally to a simple-entire form) that has accompanied the evolution of ferns into the tropical xeric environments. The other is the evolution of the climbing and scrambling leaves (pinnate-indeterminate form) that are well adapted to an ecological niche. Less important lines of adaptive evolution have developed the characteristic leaf forms of tropical alpine ferns and aquatic ferns. Other developments in the evolution of leaf form, for example, the trend toward simplification of the lamina and the development of the helicoid, radiate and furcate forms in the tropical mesic environment, do not seem to have adaptive significance.

The evolution of the same or similar leaf form in often distantly related genera is rather frequent within the Filicopsida and is largely an adaptation to a common environment. This is a striking demonstration of convergent evolution and diminishes the utility of leaf form for establishing phyletic relations.

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FIGS. 1-8: Fig. 1. *Adiantum pulverulentum*, leaf. Fig. 2. *Adiantum reniforme*, leaves. Fig. 3. *Adiantum pedatum*, leaf. Fig. 4. *Cheilanthes radiata*, leaves. Fig. 5. *Schizaea dichotoma*, leaf. Fig. 6. *Gleichenia jamaicensis*, portion of a leaf. Fig. 7. *Blechnum volubile*, portion of a leaf (the rachis bent several times). Fig. 8. *Adiantum Lorentzii*, leaf. All X 1/7.

FIGS. 9-18: Fig. 9. *Adiantum latifolium*, leaf. Fig. 10. *Saccoloma domingense*, portion of a leaf (one pinna). Fig. 11. *Notholaena sinuata*, plants. Fig. 12. *Pellaea sagittata* (var. *cordata*), plant. Fig. 13. *Notholaena standleyi*, plant. Fig. 14. *Pityrogramma triangularis*, leaves. Fig. 15. *Adiantum digitatum*, portion of a pinna. Fig. 16. *Polypodium polypodioides*, plant. Fig. 17. *Polypodium angustifolium*, plants. Fig. 18. *Vittaria lineata*, plant. All X 1/7

FIGS. 19-27: Fig. 19. *Pyrrosia lanceolata*, plants. Fig. 20. *Drynaria Fortunei*, leaf. Fig. 21. *Jamesonia cancscens*, plants. Fig. 22. *Papuapteris linearis*, leaves. Fig. 23. *Dryopteris spinulosa* (var. *americana*), leaf. Fig. 24. *Lindsaea bifida*, plant. Fig. 25. *Lindsaea lancea*, leaf. Fig. 26. *Lindsaea Ulei*, leaf. Fig. 27. *Lindsaea reniformis*, plants. All X ½.

Evolutionary patterns of living ferns

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What was the immediate ancestor of ferns like? Fossils have been of little help in answering this question. The lamentable practice of hardening hopeful speculations into formal nomenclature in names like *Protopteridium*, *Archaeopteris*, *Protosalvinia*, and Coenopteridales may give a misleading impression. An intuitive inclination to associate or not to associate a given fossil with the ferns may even tend to blind us to facts about the living ferns. For example, to think that such and such a fossil is not a fern because it possesses bordered pits, or because it has secondary growth, or collateral petiolar strands, or eusporangia, is not necessarily valid; the broad patterns of living Filicineae include all of these characteristics and more. The following discussion illustrates a deduction of the attributes of the direct ancestor of living ferns by examining their character-patterns, hopefully without prejudice, and using other living pteropsids as the major source of outside evidence. Whether or not the conclusions that result actually do prove to be borne out by future studies, the consequences of this line of reasoning seem fruitful and suggestive enough to warrant a more detailed exploration.

Such patterns as we can construct of the origin and evolution of the ferns are based almost exclusively on data from the living members of the class. There are currently two inter-related reasons why fossils have provided us with so little help. First, the majority of specimens are, as would be expected, fragments—"fern-like" stems, or leaf parts, or sporangia. We can only assume that perhaps the rest of the plant was fern-like too. But this is only guesswork and can be dangerous since so many fern-like features are repeated in other, widely different vascular plant classes. In living ferns we have theoretically all of the characteristics of their biology, structural and functional, for comparison.

The second reason illustrates the first. A number of promising fossils have become less "fern-like" as we have learned more about them in the past few decades. By the Carboniferous several fern families were in evidence—Gleicheniaceae, Osmundaceae, Schizaeaceae, and Marattiaceae.

[1] This article was prepared in connection with National Science Foundation Project G–10846. I appreciate the helpful comments of Dr. C. A. Arnold and Messrs. D. B. Lellinger and C. N. Miller, Jr.

Those fragments that we have closely match their representatives today. Prior to the Carboniferous, however, there is nothing that can now be certainly considered a true fern except by fairly extensive morphological extrapolation. The new information of recent years has made less likely any direct relationship of these pre-Carboniferous plants to the main stream of the Filicineae. The Devonian *Archaeopteris*, for example, was evidently heterosporous and anatomically specialized. There are various questions as to whether it was near the modern fern line at all. I believe it possible in view of the heavy stem-like "midrib," the form and arrangement of the rachial and terminal segments, and the peculiar position of the "stipules," that its "frond" was perhaps a dorsiventral shoot system arising in the axil of a bract. Perhaps the suggestion that this plant is a pro-gymnosperm is the best one, if it is made clear to which of the groups of "gymnosperms" *Archaeopteris* is "pro-."

The so-called Coenopteridales, if they were properly ferns at all, were likewise apparently specialized types. Where they have "leptosporangia" these are radically different from any we know in ferns, being complex structures of large size, borne in clusters on stem-like bodies (Mamay, 1957). Their stelar shapes, symmetrically complicated and provided with such peculiarities as peripheral loops, are wholly divergent from those of unquestioned Filicineae. The plant habit was probably that of a shrub, with a curious relationship between various categories of axes and much more intricate than the normal habit of a fern. *Protopteridium* is a nondescript sort of plant that could, in my opinion, be called a psilophyte as readily as a fern. The discovery (Høeg, 1942) of "axillary tubercles" in this genus casts doubt on whether the stems were actually dichotomous; they have been falsely dichotomous.

The fact that the fossil record has so far failed to throw little real light on the evolution of ferns comes as no surprise to plant evolutionists. Surely the situation in the flowering plants is still the same "abominable mystery" as ever. The angiosperms first appeared in the fossil strata of roughly 140 million years age; the ferns in strata of roughly 240 million years age. The problems of working out their evolutionary divergences are much alike. The living diversity is still our major evidence for the ancestral ground plan.

The data available in living ferns are good. Fortunately we have on the earth today a broad diversity of types and many evolutionary lines. There are some ten thousand species in three well differentiated orders—the Marattiales, the Ophioglossales, and the Filicales (the last including the heterosporous water-ferns). Some of the living forms show little specializa-

tion, as for example, *Angiopteris*, *Botrychium* subg. *Sceptridium*, and *Osmunda*. The majority of ferns, however, are more divergent. Many of the most specialized, like the Marsileaceae, the Hymenophyllaceae, and the Grammitidaceae, show contrasting pathways of divergence that give helpful radii for the establishment of central and primitive conditions.

In my opinion it is easy to overlook the obvious fact that many so-called "modern ferns," i.e., living genera and species, are very primitive types that co-exist on the earth today with extremely specialized types. We can compare such extremes as *Osmunda* and *Azolla* to illustrate this point. In fact, many ancient plants were evidently more specialized and divergent from their common stocks than many of their relatives of modern times. This probably applies to other sub-divisions such as Sphenopsida and Lycopsida with as much force as the Pteropsida. *Lepidodendron* of ancient times is apparently more specialized than the living *Selago* group of the genus *Lycopodium* today.

The broad evolutionary patterns of the ferns must be determined without reference to time and place. Only after the basic systematic correlations of divergence are found can the problems of distribution of plant variation and evolution over time and space ("phylogeny" in its most pure sense of "race history") be solved. Phylogeny must thus be based upon the systematic correlations, and it does not matter to the primary correlations themselves when and where biological change took place. The only critical initial questions are those of resemblance, sequence, and divergence in ensembles of characteristics that ultimately represent the pattern of change in genotype. As various combinations of primitive and specialized vascular plants existed since their beginnings, more or less mixed in the floras of all time levels and all geographical areas, evolutionary patterns can only be derived independently of time and place, whether the data come from fossils or living plants, from northern or southern hemisphere. In angiosperms and ferns our evidence has had to come from the living diversity simply because the fossil rocks, as stated above, have not yet yielded enough additional and reliable facts.

The recent concern of evolutionists with such problems as computer taxonomy and the principles that underlie evolutionary correlation is generating more and more powerful methods of making our conclusions objective and certain. Methodical character-by-character analysis and synthesis may take some of the mystical fun out of evolutionary speculation, but it may be expected to lead to more valid scientific results in the end. The visual ground plan correlation method which I devised a few years ago is one example of this approach (Wagner, 1961, and illustrated by Mickel,

1962). Such a method deals exclusively with the patterns of relationship and evolution. It is designed to show simply the most probable directions of genetic change, and to establish lines of relationship on the basis of multiple correlations. The broad pattern to be described below is only a preliminary one and shall require further evidence and analysis.

Operationally there should be three steps involved in working out the evolutionary patterns of ferns—(1) assortment into groups or taxa; (2) determining the trends in attributes or character-states, using correlations within the group (Filicineae) and outside the group (other classes of pteropsids and other vascular plants), supplemented by independent evidence derived from morphological sequences, ontogeny, and teratology; and, finally, (3) synthesizing the usable (the reliably correlated), character patterns into the most probable scheme of divergence lines. Our accuracy depends on the completeness of the record of evolutionary change, including all materials from whatever position in time and space: the variety and exhaustiveness of the comparative biological data used—ideally from all parts of the life-cycle; and the precision of the method of correlating the trends in characters.

In studying the patterns of living ferns according to this plan we can establish at least ten attributes of the immediate ancestor of the group with what I believe to be a rather high degree of probability. Before listing them, however, mention should be made of certain character-states, often considered to be primitive, which seem to show no definable patterns. With regard to *sporangial position*, for example, I am not convinced that the marginal position was a necessary attribute of the immediate ancestor of ferns (Wagner, 1954). It seems to have been a fluctuating state, varying back and forth from abaxial to marginal, and was probably an unstable character of the common stock. I am less assured now than previously (op. cit., p. 9) that *protostely* is an ancestral feature, for the reasons to be expanded below. Whether or not the chronologically earliest tracheophytes were protostelic in their beginnings is not the question. We can be concerned here only with the most probable conditions of the immediate fern ancestors.

To return to those attributes for which there does seem to be strong correlative basis for judgment, they are as follows:

1. **Habitat terrestrial.** The aquatic and epiphytic modes of life are evidently derived from an original condition of growth upon the soil of the ground.

2. **Spores monomorphic.** The broadest correlations indicate that heterospory is most probably a derived state. It occurs in only three families

of Filicales (Marsileaceae, Azollaceae, and Salviniaceae). Outside comparisons also tend to confirm that homospory was primitive.

3. **Spores tetrahedral without perispore.** Perisporial, more or less bilateral spores are specialized, and are characteristic especially of asplenioid and aspidioid Filicales. Non-perisporial monolete spores are scattered among ferns.

4. **Gametophytes photosynthetic.** Parasitic or saprophytic systems of nutrition are specialized. Endosporic or mycorrhizal gametophytes are exceptional in ferns at large.

5. **Sex organs large, more or less sunken.** Small, protruding gametangia are derived, and reach their extreme in the antheridia of higher Filicales.

6. **Leaf blades midribbed.** Whether the midrib of fronds is interpreted as the morphological result of lateral foliar branching or modified dichotomy is irrelevant. The correlated evidence seems overwhelming that the megaphylls of immediate filicinean ancestors, by whatever morphogenetic process, had midribbed blades (cf. Wagner, 1952).

7. **Laminar veins free.** Closed or reticulate venation patterns are of various types, arise in different ways, and in various lines; but all major groups possess some members that retain the open primitive state of venation.

8. **Trichomes simple.** Narrow, filamentous, uniseriate hairs are central to a wide spectrum of divergent trichome types, including scales, dendroids, and glandular combinations.

9. **Sporangia simple, solitary or clustered and developing simultaneously.** Gradate or mixed soral divisions are specialized, reaching their ultimate in the acrostichoid mixed sori of various families of Filicales.

10. **Sporangia massive.** The hair-like sporangia with well marked "annuli" or dehiscence bows are derivative. Typical leptosporangia of many Filicales contrast strongly with eusporangia in their highly distinctive, delicate structure and initial segmentation, but there is a gradient between the primitive and specialized states.

Certain families and genera of ferns have more of these primitive character-states than others, and are the least divergent taxa, the ones nearest the ancestral stock. The Ophioglossaceae, Marattiaceae, and Osmundaceae include the most primitive forms. All of the other families of Filicineae comprise members with totals of specializations reaching a higher order and involving several or more of these characters.

It is necessary now to face the fact that in the Ophioglossales and Marattiales, the orders of typical eusporangiate ferns, there are certain attributes that we do not find, as a rule, in the order Filicales, the more specialized,

leptosporangiate types of ferns. The question is whether these attributes are primitive or derivative. Unquestionably specialized character-states are found in the leptosporangiate ferns mostly as more or less isolated occurrences—the "upside-down" sori of maidenhair ferns, the rootlessness of certain filmy-ferns, the bracket heterophylls of staghorn ferns, and so on. In the eusporangiate ferns too, such attributes as the mycorrhizal, hairless roots, and the fertile spikes or fused fertile basal pinnae of the Ophioglossaceae, and the pulvinate leaf-blades of the Marattiaceae, are likewise unusual for ferns as a whole, as well as pteropsids in general, and are almost certainly specializations. The other, more critical character-states of the eusporangiate ferns are those which at first seem specialized when compared with leptosporangiates but which, when compared outside the Filicineae, give evidence of being actually primitive. They remind us of such angiospermous character-states of ranalean dicotyledons as "open" carpels, leaflike stamens, vesselless wood, and monosulcate pollen grains in being unusual and seemingly aberrant for the total scope of the plants concerned.

In evaluating these more questionable character-states, to be listed below, two general precepts should be taken into consideration: (1) Primitive attributes tend, in general, to be positively correlated with other primitive attributes. (2) A corollary of the foregoing—as we recede into more and more generalized plant types along two backwardly confluent lines of the same common ancestry, they tend, of course, to become more and more alike. Both of these operational principles are necessary consequences of the theory of divergent evolution. To give a concrete example, in angiosperms it now seems well established that the primitive dicots tend to share far more characteristics with the monocots than do the more specialized dicots. The primitive members of the two lines, monocot and dicot, are thus more similar than are the specialized ones.

As for the ferns, if it is true, as practically all morphologists have argued over the past half-century (e.g., Campbell, 1930; Coulter and Chamberlain, 1935), that the nearest filicinean relatives alive today are the seed-bearing cycads, then the more primitive ferns should obviously be more cycad-like than the more specialized ones. This evolutionary probability should have some bearing on the interpretation of the following character-states of the eusporangiate ferns, those for which we have no other basis to judge whether their nature is primitive or derivative:

1. **Gametophytes massive.** The gametophytes of cycads, especially the female gametophytes, are among the largest of all the pteropsids that form seeds.

2. **Embryos endoscopic.** This attribute of *Botrychium* Subg. *Sceptri-*

dium in the Ophioglossaceae and those Marattiaceae that have thus far been examined is like cycads and all other seed-plants for which we have information.

3. **Stems upright, simple, round.** Eusporangiate ferns rarely produce the elongated, branched, diageotropic rhizomes so widespread among the different lines of the Filicales. In stem habit the Ophioglossaceae and Marattiaceae are more like the Cycadaceae.

4. **Cortical parenchyma non-sclerified.** The well known "fleshiness" of eusporangiate ferns, found also in cycads, is replaced in the majority of higher ferns by extensive differentiation of endodermal and cortical mechanical tissue.

5. **Ectophloic siphonosteles or eusteles.** This condition in many Ophioglossaceae is like that of cycads and other seed-plants more than other ferns, Marattiales and especially Filicales, where we find a striking array of strictly primary patterns.

6. **Stem growth by cambia.** The stele of certain Ophioglossaceae is more similar to certain Cycadaceae than to most other ferns, and both vascular and cork cambia are present. This is entirely unlike higher leptosporangiate ferns.

7. **Tracheary pits circular.** Such pits are abundant in the tracheids of Ophioglossaceae, occasional in Marattiaceae (Bierhorst, 1961), but essentially absent in either protoxylem or metaxylem of more highly evolved ferns. Filicales tend to have scalariformly pitted tracheids and mechanical thickening contributed by the surrounding cortical sclerenchyma.

8. **Mucilage ducts.** These structures, so common in Marattiaceae, are found also in cycads and ginkgos. Further comparisons should be made of this somewhat surprising, apparently mutual resemblance to find the extent of the similarity.

9. **Stipular outgrowths or wings.** The more or less modified and conspicuous lateral dilations of petiole bases are known not only in the eusporangiate orders but in primitive Filicales (viz. Osmundaceae). Similar lateral petiole-base outgrowths in the Cycadaceae and notably in *Zamia* are well known.

10. **Collateral petiole bundles.** Certain species-groups in *Botrychium* and *Ophioglossum* are dissimilar to other ferns in showing collateral rather than concentric bundles (Ogura, 1938, pp. 290-294). They resemble seed-plants in this respect.

It must be significant that such a series of at least ten characters, a number of them of strikingly detailed nature, are shared by primitive Filicineae with the Cycadineae. It is probably no coincidence either that

the cycads themselves show a corresponding confluence of attributes with the primitive ferns. No other living seed-plants, for example, have such *frondose trophophylls* that are so similar to those of ferns. No other living seed-plants have such *fern-like sporophylls* as those of the ovulate apparatus in *Cycas*. The microsporophylls have *simple sori*. Cycads have *petiolar bundles U-shaped* in over-all outline (cf. McLean and Ivimey-Cook, 1951, p. 718) an apparently basic state in the ferns. The buds, young leaves, and sporophylls are covered with woolly indument of *narrow, filamentous, uniseriate hairs*. Cycads also have *motile, multiciliate spermatozoids*. In spite of the several cycad modifications, such as altered venations in the leaflets and the system of inter-connected changes involved in the spermatophytic type of life-cycle, a point-by-point comparison of the cycads with primitive ferns seems to show, in fact, a taxonomic gap of less distance than that which we find between the most primitive and at least certain ones of the most specialized ferns.

Those characters of the Ophioglossales and Marattiales that correlate negatively with the higher ferns but positively with the seed-plants, in particular the cycads, are probably of evolutionary meaning for the theoretical reasons given earlier. That all or the majority of these attributes of eusporangiate ferns could have evolved separately and independently from the same or similar characters in cycads is unlikely. More reasonably these character-states indeed existed in the immediate ancestor of the Filicinae, and the ancestral ferns did have a number of "cycad-like" characteristics.

That the most primitive living ferns and most primitive living seed-plants of closest relationship are more alike than the advanced members of either group is precisely what we should expect according to the theory of divergent evolution. The immediate ancestor of the ferns probably had the majority if not all of the twenty-five attributes shown in Fig. 1. The details of the pattern shown there deserve, in my opinion, careful scrutiny and re-examination. If we find no errors in detail and methodology, then we may conclude that we are dealing here with a reconstruction of the ancestor of ferns. If the theory is correct, we have more immediate evidence of a fern-cycad relationship, surely, than we do, for example, of an affinity of ferns with such fossils as *Protopteridium*, *Archaeopteris*, or *Botryopteris*. Of fossil remains other than the unquestioned ferns in the taxonomic sense, the pteridosperms probably came closer to the main stock of ferns than any other materials yet uncovered by the plant geologist.

A consequence of the above correlations, if they are correct, is the somewhat unexpected probability that the majority of ferns have become in

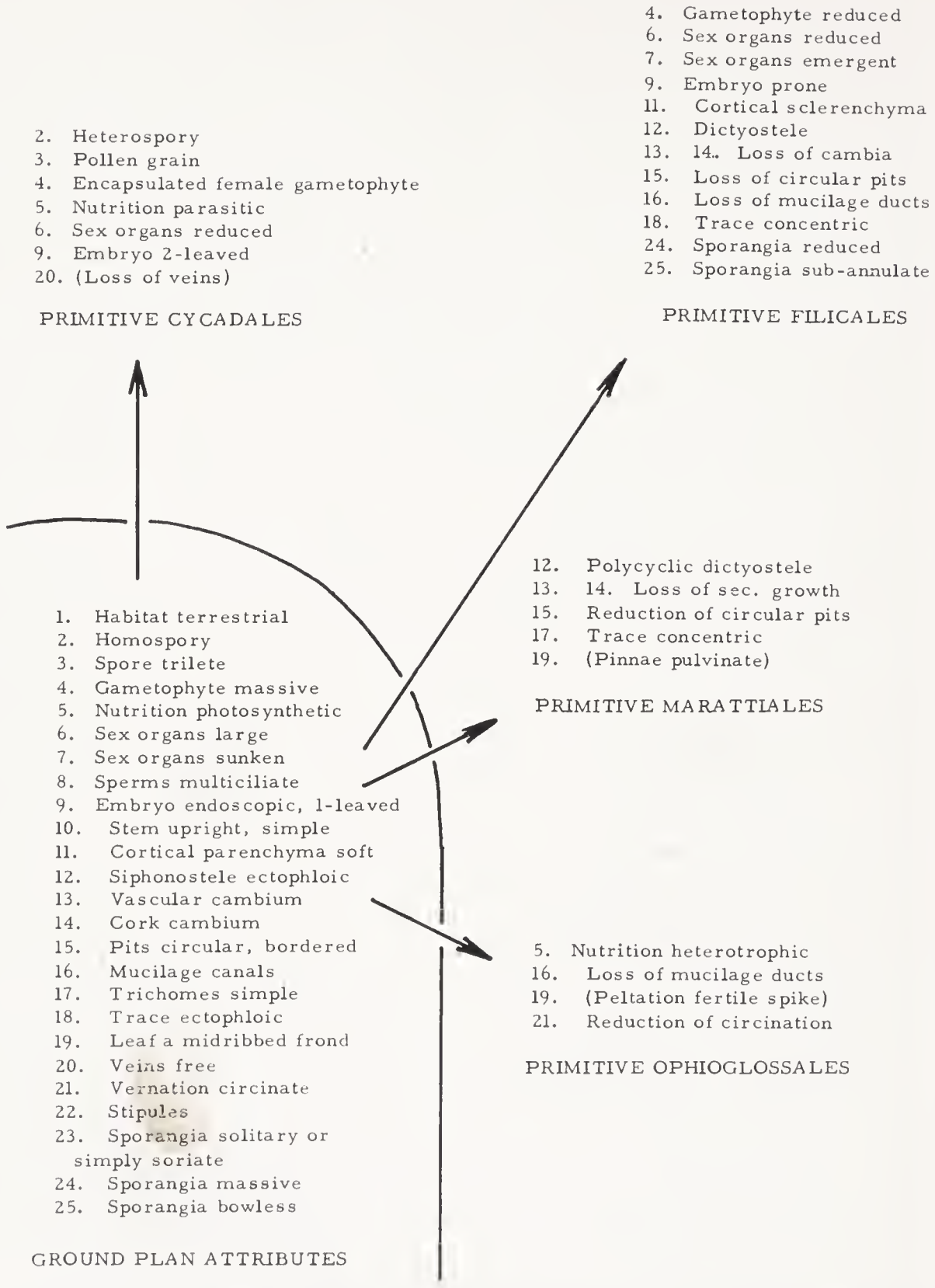

FIG. 1. Chart showing character divergences of most primitive living members of four orders from a reconstructed immediate ancestor.

stem structure rhizomatous herbs with primary growth only, like "pteridophytic monocots"—that is, strictly rhizomatous herbs or their modifications in which the original eustelar stem condition with secondary growth has undergone replacement by various arrangements and fusions of leaf traces supplemented by sclerenchymatous changes in the cortex, these transformations yielding the great variety of different cross-sectional rhizome patterns that are so widespread in these plants at different time levels since the Carboniferous. The other most pervading specializations of the ferns have involved the traditionally agreed upon changes in the reproductive apparatus, the extreme reduction and refinement of the spore-producing capsules and concomitant alterations of the prothallia and sex organs.

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